Understanding the response of a woodland-dependent mammal to habitat loss and fragmentation in the Midlands bioregion, Tasmania

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Declarations

The work presented in this thesis is original material; it has not been submitted for any degree of diploma at any university or organisation. All contributions to the completion of this work has been duly acknowledged in the thesis. None of the material contains copyright infringements.

Chapter two has published in the *Journal of Landscape Ecology*. Chapter three has been submitted and is currently in review with the *Journal of Ecology and Evolution*. Chapter four has been submitted and is in review with the *Journal of Ecology and Evolution*. All material is available for loan and limited sharing in accordance with the Copyright Act 1968 given the final decision of the journals.

The study was conducted in the Midlands bioregion of Tasmania, Australia. Methods and samples were approved by the University of Tasmania Animal Ethics Committee (Permit A14879) and the Department of Primary Industries, Parks, Water and Environment (Permit FA 15118).

The research thesis abides by all Australian codes of human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University of Tasmania.

Signed,
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31st of March 2019

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Abstract

Habitat loss and fragmentation are the leading cause of global biodiversity decline, with agricultural expansion being the dominant driver. The socio-economic importance of agriculture, together with growing human population and resource demand, is expected to result in a further one billion hectares of land being converted for agriculture and crop land by the year 2050. Species are increasingly being restricted to smaller remnants of their original range, in habitats that have undergone significant ecological change. It is increasingly acknowledged that protecting habitat is not sufficient to protect biodiversity, and instead ecological restoration will become more important for biodiversity persistence. For ecological restoration to be successful, a grounded and detailed understanding of species responses to fragmentation is needed.

Over the last 240 years, the Australian mainland has experienced the greatest loss of mammalian diversity and abundance of any comparable land area in the world. This is largely due to the introduction of invasive predators, loss of habitat and changing fire regimes. The mammalian species most at risk fall within the 'critical weight range' (CWR) of 35-5500g (Woinarski, Burbidge & Harrison 2014; Woinarski, Burbidge & Harrison 2015b). Many CWR species are threatened or near extinction. The island state of Tasmania is believed to have secure populations of CWR mammals, mainly because of the absence of the red fox in Tasmania. However, CWR mammals in Tasmania also face pressures from habitat conversion and other disturbances, especially in the agriculturally dominated Midlands bioregion. Little is known regarding the distribution and response of CWR mammalian species to such stressors. Current management efforts are in place to restore native vegetation in the Midlands to promote connectivity for wildlife. This project focuses on a critical weight range mammal, the eastern bettong (*Bettongia gaimardi)*, to provide essential knowledge on the fundamental ecology of the species needed to plan management and restoration of habitat.

The first aim of this study was to determine the distribution of the eastern bettong across the Midlands bioregion and identify habitat attributes influencing the probability of presence. A landscape-scale camera survey was carried out using 62 sites, repeated in summer and winter. Using occupancy modelling, I modelled habitat and landscape features to determine what variables predicted the presence of eastern bettongs. My analysis was designed to evaluate the predictions of alternative hypotheses on the effects of habitat loss on the persistence of species: the Island Biogeography (or metapopulation) hypothesis suggests that the occurrence of species will increase with patch size, and decreased patch isolation; the Habitat Amount hypothesis suggests that occurrence will increase with the amount of habitat available in a landscape (at a scale relevant to the movement capacity of individual animals), regardless of its patchiness. Occupancy was best explained by habitat amount within a 1km buffer rather than by patch size and isolation, together with the quality of the available habitat (quality was indicated by the density number of regenerating stems of canopy trees). These results highlight the value of small patches in fragmented landscapes for species such as the eastern bettong, and the significance of the quality of those habitat remnants.

The second chapter focuses on providing a mechanistic understanding of how the eastern bettong responds to fragmentation through variation in home ranges in fragmented landscapes. I used GPS tracking of 24 individuals across three different fragmented sites to describe variation in home ranges, and I modelled the effects of home-range size on the quality, amount and fragmentation of habitat within radii of 750 m and 250m from the mean centre of activity of individual home ranges. I also estimated population density using spatially-explicit capture-recapture analyses at the three sites, and for comparison an additional protected area with a large tract of continuous habitat. My results showed that habitat quality, the amount of woodland and population density were the most important determinants of home-range size, while there was no

effect of fragmentation. Habitat quality was the strongest determinant: home ranges were smaller in areas of higher habitat quality. On the other hand, bettongs increased their home-range size with higher density and greater amount of woodland. These results suggest that fragmentation does not limit home-range size of bettongs, who can compensate for fragmentation by increasing their ranges to incorporate more patches provided there is enough woodland accessible to them, but that quality is crucial for habitat use and therefore persistence. However, population density was lower in fragmented than in intact, contiguous woodland. Furthermore, large variations in bettong density across sites suggests habitat area is important for bettong persistence, and knowledge of baseline density is important for conservation and management.

In the last chapter, I provide a finer scale understanding of bettong habitat use and selection by investigating the movement pathways of 24 GPS tracked individuals across three sites. In the first study to use state-space modelling (Hidden Markov Modelling) on a small terrestrial mammal, I identified three distinct behaviour states based on movement patterns: denning, foraging and fast travelling. Transitions between behaviours were associated with the density of vegetation and the percent of woodland cover. Bettongs foraged in woodland and denned in areas with greater vegetation density but lower woodland cover. Across sites, bettong movements differed according to the availability of high-quality habitat. Moreover, movement of individual bettongs was not hindered by fragmentation as they readily crossed gaps, but their gap-crossing potential was improved by the presence of low vegetation and or stands of trees.

My results suggest that the eastern bettong is able to persist in the Midlands bioregion with the current extent of fragmentation and patch degradation. However, there is still cause for concern over the future of the eastern bettong in this region. Estimates of population density suggest bettongs are sensitive to habitat quality decline associated with the further risk of habitat loss and

fragmentation. To improve the population status of bettongs in the Midlands, restoration efforts should focus on improving the quality of woodland remnants and adding to the total amount or area of woodland habitat. Where habitats are degraded, restoration by planting vegetation to increase the biomass of fine roots (for example: *Lomandra longifolia*, Eucalyptus sp, Acacia sp.) can promote the growth of ectomycorrhizal fungi, which are the major food resource for bettongs and therefore increase the chance of persistence of bettong populations. Ensuring there is a high density of low-cover vegetation will provide nesting material for animals, while also providing areas that could be used by animals when crossing gaps between isolated woodland patches. Finally, many of the sites within which bettongs are found are under covenant protection giving these sites protection from disturbances such as grazing and fire. Using covenant sites as focal points for restoration and promoting their connectivity, could be an avenue of preserving and increasing the amount of high-quality woodland, which would benefit bettong populations.

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1. General Introduction

The Midlands bioregion in the summer of 2016, depicting pasture, scattered woodland and canola crop.

1.1 The Conservation Challenge

Habitat loss and fragmentation are leading causes of biodiversity decline worldwide, and present a global challenge for conservation managers (Fahrig 2002; Fahrig 2003; Mazerolle *et al.* 2006; Martin Österling & Söderberg 2015). The greatest driver of land change is agricultural expansion (Fahrig 2003; Flynn *et al.* 2009; Chaplin-Kramer *et al.* 2015; Haddad *et al.* 2015; Tilman *et al.* 2017), resulting in conversion of terrestrial native vegetation into simplified cropland or pastures for grazing livestock. Global agriculture and cropland currently covers an area similar to the continents of South America and Africa combined (Foley *et al.* 2005; Kehoe *et al.* 2017). It is likely that an additional 1 billion hectares of land will need to be converted by 2050 to support increasing global food demand (Laurance, Sayer & Cassman 2014). The conversion of land results in increased human infrastructure, human-wildlife conflict and reduction of native vegetation (Butchart 2010; Newbold *et al.* 2015; Tilman *et al.* 2017). As a result, wild animals tend to be restricted to smaller and more degraded patches of habitat, which have undergone substantial ecological modifications. The persistence of many species will rely on effective conservation management of remnant habitat.

Conservation actions aim to achieve long-term protection and maintenance of biodiversity and their ecosystems (Rodrigues *et al.* 2004). This has commonly been achieved by establishment of protected areas. Unfortunately, protected areas cover only 12% of the world's total land surface (Joppa, Loarie & Pimm 2008; Saura *et al.* 2017). Furthermore, many reserves are too small or isolated to sustain their original biodiversity, the locations of reserves are biased to regions where human populations are low, and many lack adequate management (Joppa & Pfaff 2009). The result is the protection of increasingly smaller populations and loss of crucial ecological processes such as predation and connectivity. As native vegetation is increasingly lost or fragmented, protecting land may not be sufficient, and restoration of habitat becomes important.

1.2 Ecological Restoration

Ecological restoration is defined as the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed (Young 2000; Suding, Gross & Houseman 2004). The ultimate goal is to restore the ecosystem to a functional state, in which it is resilient to further disturbances (Urbanska, Webb &

Edwards 1997; Smallwood 2001). Meeting this goal requires the presence of functional groups necessary for long-term ecological stability (Ruiz-Jaen & Mitchell Aide 2005), such as keystone species and ecosystem engineers. In particular, it requires that restored plant communities contain the elements of species composition and vegetation structure and pattern that are needed to provide habitat for the animals originally present at a given site. Often, restoration efforts have focused heavily on revegetation (Suding, Gross & Houseman 2004), relying on the presence of major elements of vegetation structure to provide habitat, and assuming that those elements of vegetation structure will provide for colonisation by animals (also known as the Field of Dreams hypothesis (Palmer, Ambrose & Poff 1997). However, decisions about what elements of vegetation to restore are typically based on human perceptions of what defines habitat, and these may well be different from the way in which animals themselves perceive habitat. The outcome can result in restoration creating 'empty habitat' that lacks significant portions of the original animal communities. It is even possible that restored habitat can set ecological traps for animals, attracting them to sites which they may be able to occupy in the short term but where they cannot reproduce successfully, or suffer excessive mortality (Hale & Swearer 2017). Because of this, conservationists acknowledge that ecological processes cannot be fully restored without understanding how animals interact with their habitat (Jones & Davidson 2016b). Specific knowledge is required for species management to ensure habitat is restored adequately. This includes understanding where a species is persisting within a landscape, how individuals select and respond to habitat and how they use their habitat in relation to the attributes available to them (Lindell 2008; Hale & Swearer 2017). Obtaining this knowledge, that conservation often fails to incorporate, provides a mechanistic approach towards restoring appropriately, which can benefit management actions (Freeman, Catterall & Freebody 2015) and promote ecosystem function and resilience.

1.3 Choosing where to restore

Choosing sites for restoration is a challenge in itself. Conservation biology often relies on the abundance and distribution of biodiversity, to determine which places should be conserved. This has often led to prioritising biodiversity hotspots such as areas of high and rare endemism (Myers *et al.* 2000), and larger contiguous habitat, as a means "to get the biggest return for every scarce dollar invested" (Norman 2003).

With increasing threats to biodiversity there is pressure to create networks of protected habitat to increase the total area of protected habitat, however this often does not take into account wildlife living outside of protected areas and often in fragmented landscapes.

In fragmented landscapes, the configuration, size and composition of remnant patches of vegetation is known to influence species distributions (Fahrig 2007a). Several different theories have been proposed as explanations for the effects of fragmentation on patterns of species richness and distribution. The classic island biogeography theory, and related metapopulation theory as first proposed by Wilson and MacArthur (1967) suggests that fragmented patches of preferred habitat are similar to islands surrounded by an inhospitable matrix, restricting species to a patch. Species richness is therefore expected to decrease with decreasing habitat-patch size and increased isolation of habitat patches (Fahrig 2002; Sodhi & Ehrlich 2010). For decades, the hypothesis shaped the understanding of species persistence in fragmented landscapes, and has been supported across a range of studies including plants (Cook *et al.* 2002), amphibians (Almeida-Gomes *et al.* 2016) and mammals (Magioli *et al.* 2015; McDonald *et al.* 2015). The theory has led to management prioritising the protection of larger patches with greater connectivity. More recently, our current understanding of species- area relationships and landscape ecology has led to the theory receiving some criticism, regarding how biodiversity may respond to changing landscapes (Cardinale *et al.* 2018). Criticism has specifically noted caveats such as the theory's relevance being bias to rare and area restricted species, overlooking many species that are not restricted by patch boundaries. More recently the island biogeography theory has been criticised as confounding the effect of habitat fragmentation with habitat loss (Laurance 2008; Fahrig *et al.* 2019).

As such this has led to recent hypotheses suggesting a less rigid theoretical framework. One such hypothesis is the habitat amount hypothesis proposed by Fahrig (2013). She highlights that species are not bound by the island theory, and therefore removes the effects of patch size and isolation. Instead the habitat amount hypothesis combines the effects of patch size and isolation and suggests species richness is a function of the total amount of habitat available in a local landscape. If applied, the hypothesis suggests management should focus on preserving as much habitat as possible regardless of configuration, and unlike island biogeography theory, places value on smaller patches of habitat.

Alternatively, the habitat continuum hypothesis (Fischer & Lindenmayer 2006) based on continuum theory suggests that all habitat within a landscape can be used to a greater or lesser extent, in which habitat is not classified binarily as 'habitat' versus 'non-habitat', instead all habitat types will vary in suitability and therefore a species should occur at varying abundances across fragmented landscapes (Fischer & Lindenmayer 2007b). These patterns of occurrence are influenced by processes such as climate, shelter, and resource abundance rather than by habitat configuration. For example, lizard populations varied gradually across fragmented landscapes as a response to changing climate and the amount of food (Fischer *et al.* 2005), rather than patch size or amount of habitat. As such, the theory suggests providing adequate resources will improve a species' persistence rather than focusing on habitat distribution.

These hypotheses are part of the larger debate regarding how habitat fragmentation is conceptualised, and therefore how biodiversity may persist in modified landscapes. As seen in articles such as "Rethinking conceptual foundations of habitat fragmentation…" by Didham, Kapos and Ewers (2012), and more recent debates "Is fragmentation good for biodiversity" (Fletcher *et al.* 2018) and the subsequent response "Is fragmentation bad for biodiversity?" by Fahrig *et al.* (2019). To some extent, the more recently proposed hypotheses suggest fragmentation may not be as detrimental as proposed by the island biogeography theory, but rather the effects of fragmentation will differ for different species and landscapes.

1.4 An animal-centric approach

The three theories of how species respond to landscape fragmentation, described above, imply different strategies of conservation management. Therefore, identifying which hypothesis best explains the response of a target species is important for their persistence and management of their habitat. Many studies highlight the impact of fragmentation in relation to species richness and biodiversity, providing a broad approach to understanding how biodiversity responds to fragmentation. This often leads to management responding with equally broad approaches. As mentioned above, a well-known example is the 'field of dreams' hypothesis, first proposed by Palmer, Ambrose and Poff (1997). Based on this, previous perception of habitat ignored the links between species and specific habitat elements required for their survival, ignoring

important ecosystem processes tied to an animal's behaviour and distribution, and therefore responses of species to habitat pattern (Henle *et al.* 2004). Understanding how an animal perceives its habitat can be important for target species to inform management decisions and restoration practices.

An animal's survival depends on its ability to find adequate resources. Movement capability and daily requirements, including for food and space, will vary among species. For example, generalists and specialists are expected to respond differently to fragmentation due to differences in their diet and niche breadth (Henle *et al.* 2004; Devictor, Julliard & Jiguet 2008; Martinson & Fagan 2014). Furthermore, species that are more mobile can utilise more of the landscape than species with smaller ranges (Doherty & Driscoll 2018a) as demonstrated in butterflies (Warren *et al.* 2001) and marsupials (Fisher, Blomberg & Owens 2003b) therefore how habitat is managed should incorporate how a species moves and utilises its surroundings. This can elucidate to what a species perceives as habitat elements important for foraging and shelter, and at what spatial scales management should focus to promote ecological processes.

Lastly, landscapes are not homogenous, and resources are likely to be distributed unevenly, and vary in quality. Recent studies have shown that quality may be more important in determining species distribution and persistence, as seen in birds (Häkkilä *et al.* 2018), wolves (Lesmerises, Dussault & St-Laurent 2012) and the success of invasive species (Didham *et al.* 2007), but what an animal perceives as high quality varies. Given the variation in species requirements, management needs to identify species- specific responses, which can be used to infer population-level requirements for more inclusive management at the landscape scale.

1.5 Decline and threat in Australian mammals

Since the arrival of European settlers in 1788, Australia has undergone exceptionally high rates of mammalian extinctions, especially among ground-dwelling species (Burbidge and Manly, 2002; Johnson, 2006). Australia has lost more than 10% of its endemic species of land mammals, and losses have been especially high in arid, semi-arid and southern temperate regions (Woinarski, Burbidge & Harrison 2015b) however recent studies have suggested declines are also substantial in the tropics (Fisher *et al.* 2014). Many species have experienced more than a 25% reduction of their native ranges resulting in local extinctions. The

loss of mammals is a result of a combination of stressors increasing rapidly over the last 230 years. The major culprit is the introduction of invasive predators, the red fox (*Vulpes vulpes*) prevalent across most of Australia apart from tropical and island regions of the country, and the feral cat (*Felis catus*) found across the entire country. They have been successful 'invasives' and as a result are continually having devastating impacts on mammal species (Johnson 2006; Woinarski, Burbidge & Harrison 2015a; Doherty *et al.* 2017). There is some evidence that the introduction of diseases such as *Toxoplasma gondii* has also contributed to the collapse of animal populations (Obendorf, Statham & Driessen 1996; Eymann *et al.* 2006; Parameswaran *et al.* 2009) however the extent of its effect on wild populations is still being studied.

Moreover, increased human activity and population growth has also led to habitat loss and fragmentation due to mining, increased urbanisation, agriculture and cropland, contributing to reducing and degrading native habitat (Fisher, Blomberg & Owens 2003a; Mackey *et al.* 2008; Ritchie *et al.* 2013). Additionally, a change in fire regimes from indigenous practices of slow, patchy burns to larger and more intense fires results in further habitat loss and damage for longer periods of time (Woinarski, Risler & Kean 2004; Lawes *et al.* 2015) resulting in the loss of ground cover for protection, in turn reducing their resources and exposing animals to greater risks of predation. Where native habitat is limited, further fragmentation becomes an important concern as this can increase disturbances, threaten the remnant amount and quality of native habitat available for native species, and inevitably has important implications for biodiversity persistence.

1.5.1 Critical weight range mammals

While probability of extinction generally increases with body size, extinctions of ground-dwelling Australian mammals are concentrated on small-intermediate body sizes, in the so-called critical weight range (CWR) of 35 and 5500g (Burbidge & McKenzie 1989; Burbidge *et al.* 2009; Murphy & Davies 2014). The term has been highly debated, after Cardillo and Bromham (2001) suggested their findings did not show support for extinction in specific weight ranges. Later, Johnson and Isaac (2009) suggested that partitioning species into their habitats and expected rainfall, showed a clear extinction risk for species falling within the CWR, especially ground-dwelling species in low rainfall areas. Since, there has been increasing evidence of population decline in CWR mammals.

Species within this range have been most affected as they fall within the suitable prey-size range of invasive predators, the feral cat and red fox. Their declines have been noted nationwide resulting in many surviving CWR mammals currently categorised as nationally vulnerable or threatened and expected to continue to decline (Woinarski, Burbidge & Harrison 2015a). Their persistence is exacerbated as their native habitat declines, and resources such as refuges and foraging habitat are challenged by agricultural expansion.

Nationwide eradication of invasive species often controversial (Doherty *et al.* 2016) and therefore current management frameworks to manage population have relied on translocation, reintroductions and fencing of protected areas to conserve CWR species. With many species living in constricted ranges managing habitat for the species may be the most effective avenue for species persistence in the wild (Doherty *et al.* 2015).

1.5.2 The eastern bettong

The eastern bettong (*Bettongia gaimardi*) falls within the critical weight range. It is a member of the family Potoroidae, weighing approximately 1.5kg. It presently occurs in eastern Tasmania in dry sclerophyll woodland and forest, and is most abundant on infertile soils (Taylor 1993a; Johnson 1994a). It is considered a woodland specialist and ecosystem engineer, providing important ecosystem services. The eastern bettong's diet consists predominately of ectomycorrhizal fungi (Rose 1986; Taylor 1986; Taylor 1992b), which associate with the roots of many shrub and tree species (Johnson 1994a). Mycorrhizal fungi assist nutrient and moisture uptake for plant species in less fertile soils (van der Heijden *et al.* 1998; Claridge 2002); the foraging and consumption of sporocarps of ectomycorrhizal fungi by the eastern bettong results in dispersal of fungal spores, and therefore maintains the ectomycorrhizal symbiosis to the benefit of both fungal and plant diversity (Johnson 1996). Additionally, the digging activity of animals such as the eastern bettong is responsible for bioturbation of soils (Garkaklis, Bradley & Wooler 1998; Fleming *et al.* 2014b), a process which improves soil condition, traps leaf litter and moisture, improves seedling growth and possibly even slows down bushfires (Garkaklis, Bradley & Wooler 1998; Valentine 2014; Hayward *et al.* 2016; Valentine *et al.* 2018).

Eastern bettongs once occurred across much of the southeast of mainland Australia from Queensland to South Australia (Wakefield 1967; Rose 1986). Like many CWR mammals, the species became

extinct on the mainland, due mainly to predation by the red fox and (possibly) feral cats (Rose 1986; Robley *et al.* 2014; Doherty *et al.* 2017; Legge *et al.* 2017), persecution by humans and habitat loss (Short 1998). The species currently persists in the wild only on the eastern half of the island state of Tasmania, apart for a population introduced to the Mulligans flat reserve near Canberra in the Australian Capital Territory (Batson *et al.;* Shorthouse *et al.* 2012). The remaining populations in Tasmania are not threatened by the red fox, where there have been no sightings or records since 1998 (DPIWE, https://dpipwe.tas.gov.au/invasive-species/programs-and-alerts/fox-eradication-program/fox-evidence-update, accessed 4/3/2019), but they face other threats. In particular, a large majority of the bettong's distribution in Tasmania falls within an agriculturally dominated landscape, where native vegetation is now severely fragmented.

1.6 Midlands bioregion

The Midlands bioregion was among the first agricultural areas settled by Europeans in Australia. It is one of eleven biodiversity hotspots in Australia (Cowell *et al.* 2013), and covers 7760km^2 of low-elevation dry woodland and grasslands (originally) in the eastern half of Tasmania (Figure 1). The region is characterised as a dry and low plateau basin, and it receives approximately 500mm of rainfall annually. It hosts a diversity of endemic species, including plants and invertebrates, but also a suite of marsupials that are either threatened or extinct on the mainland of Australia. These include three predators, the Tasmanian devil (*Sarcophilus harrisi*), spotted tailed quoll (*Dasyurus maculatus*) and eastern quoll (*Dasyurus viverrinus*); the herbivorous eastern bettong and Tasmanian pademelon (*Thylogale billardierii)*, and the omnivorous eastern barred bandicoot (*Perameles gunnii*). Originally, the region was a mosaic of dry sclerophyll woodland and forest and expanses of native grasslands but it has undergone extensive conversion of native vegetation. The bioregion is currently dominated by pasture for livestock production (sheep and cattle), some cropping of cereals such as wheat and rapeseed, and increasing areas of irrigation for high-value crops such as medicinal opium and pyrethrum (Jones & Davidson 2016b).

The remnant vegetation of the Midlands is highly fragmented, an estimated 10% of native woodland and 3% of native grassland remain from the original habitat (Jones & Davidson 2016b). Most of the native vegetation is on private property and only 2% of the area is under protection. Moreover, threats from invasive

species such as gorse, willows, deer and feral cats are also prominent across the region (Department of Primary Industries Water and Environment (DPIWE): http://www.environment.gov.au/biodiversity/conservation/hotspots/national-biodiversity-hotspots#hotspot4 accessed 6/6/2018).

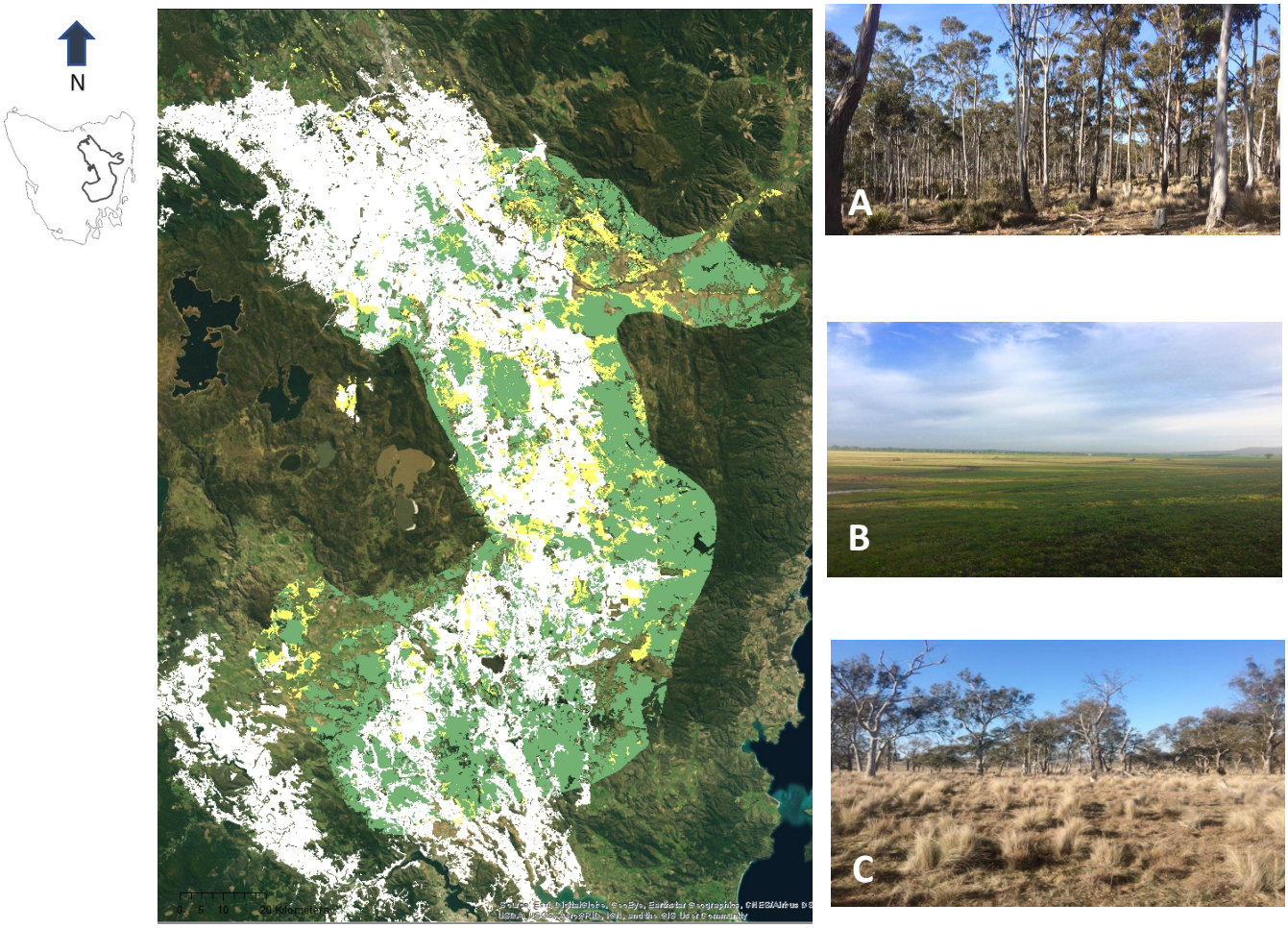

Figure 1. An outline of the Tasmanian Midlands bioregion, and broad land use categories using TASVEG 3.0 showing woodland in green (A), agriculture in white (B) and native grassland in yellow (C)

1.7 Project aims

Several non-government organisations – Greening Australia Tasmania Inc., Australian Bush Heritage and the Tasmanian Land Conservancy— are working with the Tasmanian government Department of Primary Industry, Parks, Water and Environment to restore and reconnect native vegetation across the Midlands

bioregion. This project aims to provide evidence to inform management efforts on how best to manage and restore remnant vegetation for the eastern bettong within the Midlands bioregion. I aimed to understand the bettong's distribution and habitat use, with specific attention to the features of fragmented landscapes that determine whether populations are able to persist.

This thesis consists of three data chapters that report my research results, as well as this Introductory chapter and a final Conclusions chapter. Each of the three results chapters is written as a paper intended for publication. The aims of these are summarised below:

Chapter 2 describes the distribution of the eastern bettong at the large scale over the entire Tasmanian midlands. In this chapter I used a camera survey to collected data on the presence and absence of bettongs at various sites distributed across the midlands, and used occupancy modelling to understand the factors – woodland fragmentation, other landscape variables, and effects of predators – that determine the patterns of distribution of the bettong. In particular, this analysis tested whether the occurrence of the eastern bettong was sensitive to the size and isolation of remnant patches of woodland, as predicted by the Island Biography/metapopulation theory, or the total amount of habitat in the local landscape, as predicted by the habitat amount hypothesis.

Chapter 3 provide a detailed understanding of how bettongs respond to fragmentation by exploring their movements in relation to habitat availability. The research examined the ranging behaviour of individual eastern bettongs in focal landscapes, to understand the way in which individuals compensate for fragmentation of habitat by expanding their home ranges, and also testing how population density and habitat quality also affect home-range size.

Chapter 4 examined how state space modelling via the collection of GPS locations could be used to identify individual bettong behaviours to gain a finer scale understanding of how bettongs may use habitat, but also understand what woodland attributes drive the transitions between these behaviours, and therefore gain an understanding of how they may perceive habitat within a fragmented landscape.

Chapter 5 summarised the findings presented in the thesis. I specifically present the benefits of using an animal centric approach to provide a finer scale understanding of the relationship between animal spatial and landscape ecology to better inform restoration efforts.

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Chapter 2: Habitat amount and quality, not patch size, determine persistence of a woodland- dependent mammal in an agricultural landscape

A curious bettong detected during our landscape scale camera surveys

2.1 Abstract

Context: The classical theory of island biogeography explains loss of species in fragmented landscapes as an effect of remnant patch size and isolation. Recently this has been challenged by the habitat amount and habitat continuum hypotheses, according to which persistence in modified landscapes is related to total habitat amount rather than habitat configuration or the ability of species to use all habitats to varying degrees. Distinguishing between these theories is essential for effective conservation planning in modified landscapes.

Objective: Identify which factors of habitat type, amount and configuration predict the persistence of a keystone woodland specialist, the eastern bettong *Bettongia gaimardi*, in a fragmented landscape.

Method: In the Midlands region of Tasmania I carried out camera surveys at 62 sites in summer and winter. I included habitat and landscape features to model whether habitat amount or patch size and isolation influenced the presence of the eastern bettong, and to measure effects of habitat quality.

Results: Habitat amount within a 1 km buffer was a better predictor of occupancy than patch size and isolation. Occupancy was also affected by habitat quality, indicated by density of regenerating stems.

Conclusion: Our results support the habitat amount hypothesis as a better predictor of presence. For a species that is able to cross the matrix between remnant patches and utilise multiple patches, the island biogeography concept does not explain habitat use in fragmented landscapes. Our results emphasize the value of small remnant patches for conservation of the eastern bettong, provided those patches are in good condition.

2.2 Introduction

Conversion of native vegetation for agriculture is a major and escalating threat to biodiversity globally (Tittensor *et al.* 2014; Newbold *et al.* 2015; Maxwell *et al.* 2016; Venter *et al.* 2016b). Agricultural land covers 38% of the land surface of the earth (Kehoe *et al.* 2017). The conversion of land for agriculture has resulted in the widespread loss or reduction of contiguous native vegetation across all habitat types, including forests, grasslands and wetlands (Sodhi & Ehrlich 2010; Johnston 2013; Haddad *et al.* 2015). The socio-economic value of agricultural production (Venter *et al.* 2016b) and growing human population will result in continuing expansion and intensification of agriculture, coupled with increased infrastructure and global human footprint (Lindenmayer & Fischer 2013; Laurance, Sayer & Cassman 2014; Venter *et al.* 2016a). Species that persist in largely cleared agricultural landscapes are often restricted to remnant fragments of habitat, which are smaller and may have undergone significant ecological modifications from their original state (Fahrig 2007b; Fischer & Lindenmayer 2007a). Understanding how biodiversity responds to the stressors of landscape modification, including decreased quality, fragmentation and loss of habitat, is important for managing persistence of biodiversity in agricultural landscapes.

Identifying features of fragmented agricultural landscapes that influence the persistence of the original native species is a significant research focus. Much effort has focussed on the effects of size and isolation of remnant patches of habitat (Haila 2002). This research was grounded in the equilibrium theory of island biogeography and the related theory of metapopulation ecology. These hypotheses assume that the target native species are unable to occupy the matrix that surrounds habitat remnants and predict that species richness increases with patch area and decreases with patch isolation (Fahrig 2002; Krauss *et al.* 2004; Laurance 2008). Patch size and isolation have indeed been reported to be important for species persistence, functional diversity and the retention of ecosystem functions in many taxa as seen in plants, invertebrates, amphibians and birds (Sahlin & Schroeder 2010; Sodhi & Ehrlich 2010; Mönkkönen, Rajasärkkä & Lampila 2014; Munguía-Rosas & Montiel 2014; Magioli *et al.* 2015; Almeida-Gomes *et al.* 2016; Seahra, Yurkonis & Newman 2016).

Recent studies have questioned the relevance of this framework for species that are able to use multiple remnant patches of habitat. This is true of many species that are primarily dependent on forests and

woodlands (Anderson, Rowcliffe & Cowlishaw 2007; Ditmer *et al.* 2015; Ripperger *et al.* 2015). For such species, persistence in a given landscape may depend on the total amount and the quality of preferred habitat that remains, as distinct from the particular configuration of patches that determines the pattern of size and isolation (Fahrig 2013; Fahrig 2017). There are two alternative hypotheses to explain species use of heterogeneous landscapes: the habitat amount and the habitat continuum hypotheses. The habitat amount hypothesis proposes the effects of fragmentation are due to a loss of available habitat. Species richness and abundance should increase with increasing total amount of habitat surrounding a site of interest, regardless of patch size and isolation. Instead, habitat amount should replace the effects of the latter (Fahrig 2013). This hypothesis has been supported by some empirical studies (Püttker *et al.* 2011; Melo *et al.* 2017; Seibold *et al.* 2017), but is not universal in its explanatory capacity. The amount of habitat explained species richness of small mammals in fragmented savannahs in Brazil, rather than patch size and isolation (Melo *et al.* (2017). Conversely, the density and species richness of plants in small fragments of grassland and birds in orchards was better explained by the island biogeography theory rather than by habitat amount (Bailey et al. 2010; Lindgren and Cousins 2017; Torrenta and Villard 2017). Alternatively, the continuum hypothesis highlights all habitats can be used regardless of configuration.

Instead, species distribution is driven by ecological processes (i.e.climate, latitude, food, shelter), and therefore occupancy occurs at a gradient within a landscape (Fischer, Lindenmayer & Kaitala 2006). For example, species richness and composition of lizards gradually varied across a fragmented landscape, explained by a variety of variables such as climate, amount of food and space rather than site area or amount of cover (Fischer *et al.* 2005). Identifying which of the mechanisms posited by these theories is operating in fragmented landscapes is essential for management of biodiversity in such landscapes.

Quality of available habitat affects persistence of species in fragmented landscapes because the extent to which vegetation patches provide food and shelter will influence population vital rates, such as survival and reproduction, and therefore abundance at a local and landscape scale (Hanski 2015). While all patches in a landscape, including native remnants and the agricultural matrix, represent potential habitat (the habitat continuum hypothesis), habitat quality will vary greatly depending on a species' habitat requirements, niche breadth and the extent of impacts that degrade the native remnants (Battin 2004; Mortelliti, Amori & Boitani 2010). Furthermore, some features of modified landscapes can act as barriers to movement (Ascensão

et al. 2017) or cause elevated mortality during movement through the matrix (D'Amico *et al.* 2015; Ruiz-Capillas, Mata & Malo 2015), and therefore limit the ability of species to gain access to remnant habitat.

In this study, I assess the pattern of occurrence in a fragmented agricultural region of a medium-sized marsupial, the eastern bettong (*Bettongia gaimardi*; Family Potoroidae). It is a solitary species, with an average home range of 0.9km^2 (Gardiner et al. *in review*). The eastern bettong is thought to be an ecosystem engineer because, like other potoroid marsupials, it modifies soil structure and fertility in the course of digging for its food (Fleming *et al.* 2014b). It is also an ecological specialist, being largely dependent on sporocarps of ectomycorrhizal fungi that associate with eucalypts, acacias, and other sclerophyll woodland plants (Taylor 1992a; Taylor 1993a). Potoroid marsupials are shown to be sensitive to patch size in fragmented landscapes (Bennett 1990), and have suffered major declines due to the impacts of invasive predators and habitat loss (Woinarski, Risler & Kean 2004; Johnson 2006). Eastern bettongs have become extinct on the mainland of Australia but survive on the island state of Tasmania, where they are distributed across the drier eastern half of the island. Within this area, their occupancy of the landscape is quite heterogeneous and they have declined dramatically in parts of their range that have been fragmented for agriculture.

This study focused on the Midlands bioregion of Tasmania, which takes in the dry, lowland (below 500 m) parts of the catchments of the Macquarie and Derwent Rivers in central-east Tasmania, Australia. One of Australia's Biodiversity Hotspots (https://www.environment.gov.au/biodiversity/conservation/hotspots/national-biodiversity-hotspots, accessed 26/02/2018), the Midlands hosts a suite of endemic plants and marsupial species that are threatened or are extinct on the mainland of Australia. It was originally dominated by native grasslands and dry sclerophyll woodlands, but more than 200 years of intensive agricultural production has resulted in conversion of approximately 90% of the original vegetation communities to pasture for sheep and cattle, and recent intensification for high value irrigated crops, such as medicinal opium. Native vegetation in the Midlands are now fragments in a sea of agriculture, with less than 10% of native woodland and less than 3% of native grassland remaining (Jones & Davidson 2016a). Remnants are heavily modified by grazing and fire. Furthermore, the feral cat (*Felis catus)*, is an abundant invasive predator across the state. It is a threat to native mammals, both as a predator and as the definitive primary host for the pathogen *Toxoplasmosis gondii* to which many marsupials have little resistance (Spencer *et al.* 2016; Doherty *et al.* 2017).

I use occupancy modelling to determine the landscape and local-scale attributes that influence presence of the eastern bettong in remnant woodland in the fragmented agricultural landscapes of the Tasmanian Midlands. In particular, I test whether patch size and isolation or habitat amount were more important in determining the species' response to fragmentation. I considered the habitat continuum theory to not be as relevant to eastern bettongs, as they don't extensively use the matrix as primary habitat. I also test whether disturbances are important in predicting the presence of bettongs. Road mortality from collisions with vehicles, pivot irrigation near water sources, and urban settlements are common in the Midlands bioregion. Lastly, as bettongs are prey for both native and invasive mammalian predators, I test whether the presence of predators - the Tasmanian devil (*Sarcophilus harrisi*), spotted tailed quoll *(Dasyurus maculatus*) and feral cat (*Felis catus*) – influence occupancy and detection of the eastern bettong.

2.3 Methods

Camera traps (ReconyxTM PC800) were used to survey occupancy of mammals, including eastern bettongs, at a landscape scale across 7,660 km^2 of the Midlands bioregion of Tasmania. Two five-week surveys were carried out, one in the austral winter between June-August 2015, and the second survey in the summer between January-February 2016.

2.3.1 Site selection

A total of 103 sites were selected to be geographically representative of the Midlands, including 62 sites in native woodland – the most common type of native vegetation remnant – 20 sites in native grassland, and 21 sites in introduced pasture. To select sites based on these broad vegetation categories, I used and combined the vegetation classifications in the state government GIS vegetation layer: TASVEG 3.0 (http://dpipwe.tas.gov.au/conservation/development-planning-conservation-assessment/planning-tools/monitoring-and-mapping-tasmanias-vegetation-(tasveg)/tasveg-the-digital-vegetation-map-of-tasmania). Much of the remnant native vegetation of the Midlands is on private property, is fragmented to differing degrees, and is unevenly distributed across the landscape. To represent the variability in patch size and isolation, I stratified woodland patches into three size categories – small (20-100ha), medium (100-200ha) and large (>200ha). I then filtered the large number of sites in each category by habitat condition, presence of

shrubby or grassy understorey, and selected equal numbers of sites from each patch size category. I differentiated native grassland from pasture sites by their dominant plant species. Native grasslands were dominated by at least 70% of native grass species including *Poa* spp, *Themeda*, *Microlina* and others. Pasture sites were chosen within paddocks dominated by introduced grass species. To provide independence for each habitat type sampled, sites were separated by a minimum of 1 km, a distance too large for a bettong to cross a matrix, however all of our sites were separated more than 1 km. I collated a total of 18 variables considered *a priori* to be ecologically relevant to the study species (Table 1). A preliminary analysis revealed that bettongs were never detected at sites in pasture, and were detected only twice at native grassland sites, both of which were close to or surrounded by woodland. Given the low detections in pasture and grassland habitats, the sites that were in pasture and grassland were removed from the analysis, which was re-run using only the woodland sites (n=62).

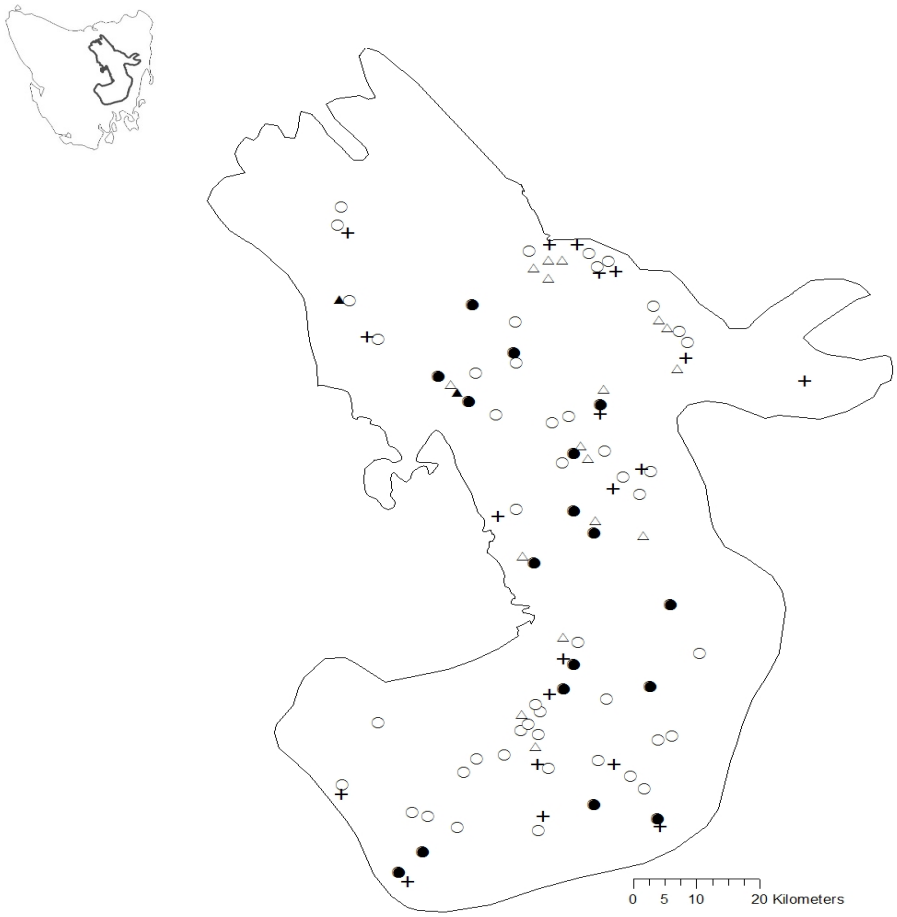

Figure 1: Outline of the Midlands bioregion in Tasmania, Australia and the spread of sites sampled. Circles represent woodland, triangles represent native grassland and crosses represent pasture sites. Filled shapes represent sites bettongs were detected.

2.3.2 Camera trapping and data handling

Cameras were set in the middle of a patch, mounted on a vertical structure - a tree, fence post or wooden stake - approximately 1m off the ground. A visual and an olfactory lure were placed 1.5m in front of the camera, with the field of view of the camera targeted below the lure. The olfactory lure was a mixture of rolled oats, peanut butter, nut oil, sardines and tuna oil, placed on the ground in a PVC canister. The visual lure was a CD suspended from a tree at a height of 1m, a method used to attract species attention (Algar *et al.* 2007). Cameras were set to take a rapid-fire sequence of 3 consecutive pictures with a 'no delay' setting when the infra-red sensor was triggered. Images were processed in ExifPro software (http://www.exifpro.com/). All animals captured in images were identified to species, if possible, and recorded with time of capture, for each survey night and site location. Images were used to construct a binary detection history; given low detections and lack of unique identifying features of bettongs I pooled detections. One or more detections within a week was scored as 1, and lack of detections were scored as 0. Images in which the species could not be confidently identified were discarded, as were false triggers. If cameras failed during the sampling period, the weeks of lost data were classed as 'NA', equivalent to not surveyed.

2.3.3 Landscape-scale variables

Landscape-scale variables were mapped and measured using TASVEG 3.0 in ArcGIS 10.2. These included patch size, patch isolation (Euclidean distance to closest woodland), distance to nearest drainage line or water body (wetland, farm dam), distance to nearest road, and the proportion of native woodland, native grassland, plantation (native restoration plantings; mostly *Eucalyptus spp.*), agriculture and urban area within a 1 km radius (buffer) of the camera site (Table 1). This buffer size is approximately equal to the typical home-range area of an eastern bettongs as reported by Taylor (1993b) and Gardiner et al. (*in review*).

2.3.4 Local-scale variables

Local-scale variables centred on the camera site were measured on 2 x 50 m transects that formed a cross with the camera site at the intersection (Table 1). Within the area of the transect, I estimated the percent cover of native vegetation in the over-storey (>5 m), mid-storey (1-5 m) and shrub (0.2-1 m) layers. To assess how bettongs might use vegetation structure to detect and evade predators, I measured horizontal visibility (VVS) five meters from the camera at each cardinal point. Visibility was measured using a $1m^2$ white sheet divided into units, held by an assistant and touching the ground. I recorded the percentage of the sighting sheet that was visible, i.e. not obscured by vegetation at each of the heights 0-25, 26-50, 51-75, 76-100 cm off the ground. For this study on bettongs, I used the average of the percentage measures at the 0-25 cm height, which is approximately the height of a bettong, at which it can visually survey its surroundings for danger. To provide an indicator of woodland health, I counted the total number of regenerating stems of *Eucalyptus* species (including seedlings, sprouts and saplings) and the total number of vegetation life forms (excluding invasive and perennial species) within 5 m of each transect. Greater numbers of regenerating stems have been suggested to indicate healthy woodland remnants with good recruitment (Bailey 2012). To assess the potential influence of predators on the occupancy of bettongs at a site, I included a matrix of detections for the spotted tail quoll and feral cat as a parameter. The Tasmanian devil was not included due to the significant decline of the species across the landscape.

Landscape	Definition
Patch Size	Total patch size in meters squared
Isolation	Patch isolation measured by distance to nearest neighbour in meters
Woodland	Amount of woodland within 1km buffer
Plantation	Amount of non-native plantation within 1km buffer
Agriculture	Amount of crop and pasture within a 1km buffer
Grassland	Amount of native grassland within a 1km buffer
Urban	Amount of urbanisation within a 1km buffer
Distw	Nearest water body including rivers, dam and lakes in meters
Distrd	Nearest named road in meters
Habitat	
Over	Percent cover of over storey trees (> 5m) within 25x25m square
Mid	Percent cover of mid storey trees (1-5m) within 25x25m square
Shrub	Percent cover of shrub species within 25x25m quadrat
Regen	Number of regenerating stems counted within 5m of the 2x50m transect
Plant Richness	Number of plant life forms- species richness- within 5m of the 2x50m transect
Vvs	Averaged vertical visibility recorded 0-25cm off the ground at each cardinal point
Predators	
Quoll	Total number of *Dasyurus maculatus* Potentially greatest threat to B.gaimardii
Cat	Total Number of *Felis catus* Introduced, disease host and potential threat

Table 1. Name and definition of patch and landscape variables used in our occupancy analysis

2.3.5 Data handling and occupancy modelling

All analyses were run in R Studio version 3.2.1 using package 'unmarked' (Fiske & Chandler 2011). Occupancy was determined using a single-species, multi-season model while accounting for detection probability, as described by McKenzie et al (2002, 2003). I did not expect changes in colonisation and extinction within one year, therefore these parameters were kept constant throughout the analysis. Prior to modelling I performed a check of normality on all landscape and habitat variables and applied transformations (z- transformations for discrete variables and log transformations for continuous variables) if necessary. A check for collinearity was performed using variance inflation factors (VIF) and a visual pairwise comparison of variables. None of the variables showed high collinearity (VIF= > 3) and therefore all were retained for analysis (Appendix 1).

First, I built and ranked models to determine factors that influenced detection probability of bettongs on any given night at a site. Iran models with null, single and combinations of the detection covariates including the age of the bait (starting at one day and increasing in daily increments until the end of the survey)

season (winter and summer), and detections of quolls and cat at each survey while keeping occupancy constant. I ranked models using Akaike Information Criterion (AIC) and examined all models that were within 2 AIC units of the model with the lowest AIC value. Where there was more than one model in the candidate set, I chose the most parsimonious model (with the fewest parameters). The parameters in the best model were thereafter incorporated into all occupancy models.

I conducted the analysis in two steps. First, Iconstructed models specifically to test and compare the two hypotheses regarding response to landscape fragmentation that are relevant to eastern bettongs: patch size and isolation, and habitat amount. To test patch size and isolation, I built single models including patch area, and distance to nearest patch (isolation). To test habitat amount, I included the total amount of woodland within 1 km of the camera location, to ensure it incorporated the majority of a bettong's home range. I also built models testing the total amount of other landscape and vegetation types within 1 km: total native vegetation, agriculture, plantation and urban area. Each model was compared and ranked to the null model (Table 3). The second step of the analysis was to include the variable within the best ranked model in all occupancy models. The rationale for including this variable, which was the amount of woodland habitat, was that initial analyses revealed such an over-riding importance of woodland habitat in describing the occupancy of bettongs that any influence of other variables was not described. I built models of single variables (in addition to the variable from the best-ranked model in the first step), followed by more complex models with combinations of variables, and ranked these using Akaike Information Criterion. Model fit to the data was assessed using McKenzie and Bailey goodness of fit within the AICModavg package (Mazerolle & Mazerolle 2017) using 1000 bootstrap samples to determine which model best-supported bettong presence in woodland habitats. I calculated the odds ratios (OR) for each variable to determine the association between presence and each of the variables (Table 4).

2.4 Results

Eastern bettongs were detected 67 times at 17 of the 62 woodland sites over the two camera surveys. The detection model that included bait age was the best-performing model compared with models including single or combinations of season, feral cats, quolls and or the null model (Table 2). The probability of

detecting a bettong decreased as bait age increased. A detection model including bait age was subsequently included in all occupancy models.

Model	K	AIC	ΔAIC
Bait	5	285.72	0
Bait+ Season	6	287.72	2
Null	4	288.67	2.95
Cat	5	288.95	3.23
Quoll	5	289.45	3.73
Season	5	290.67	4.95

Table 2. Model ranking of detection covariates which could influence Eastern bettong presence, and incorporated into occupancy modelling.

Ψ	*p*	K	AIC	ΔAIC	AICwt
Woodland	Bait	6	279.23	0	0.866
Null	Bait	5	285.72	6.49	0.034
Isolation	Bait	6	286.69	7.46	0.021
Agriculture	Bait	6	286.75	7.52	0.02
Grassland	Bait	6	287.03	7.8	0.018
Plantation	Bait	6	287.22	7.99	0.016
Patch size	Bait	6	287.58	8.35	0.013
Urban	bait	6	287.72	8.49	0.012

Table 3: Model ranking testing the importance of patch size and isolation versus habitat amount in determining Eastern bettong presence in a fragmented landscape.

The amount of woodland habitat in a 1 km radius of the camera site was the only model of the eight single parameter models run in step one of the analysis that described the relationship of occupancy to habitat amount and distribution (Table 3). Occupancy of bettongs was positively related to amount of woodland habitat within that radius. All other models were at least 6 AIC values more than the best model suggesting that patch size and patch isolation were not as important in predicting presence as the amount of woodland (Figure 2). Similarly, the amount of pasture, plantation and native grassland within the buffer were not important predictors; all showed trends of decreasing presence of bettongs with increasing amount of pasture, plantation, urban settlement and native grassland within a 1 km buffer of the camera location.

Variables	Ψ
Cat	0.122
Grassland	0.131
Devil	0.137
Agriculture	0.182
Plantation	0.210
Shrub	0.308
Mid	0.382
Urban	0.388
Vvs	0.388
Size	0.485
Quoll	0.5
Over	0.820
Plant richness	1.110
Distrd	2.111
Regen	3.586
Distw	3.639

Table 4. The odds ratios for the relationship between variables and occupancy probability (Ψ). Odds ratios more than 1 indicate increased likelihood as the covariate increased, while odds ratios less than 1 indicate the covariate is less likely.

When the amount of woodland was retained in all models, there were two competing models in the final candidate set (within 2 AICs). The top model, which carried more than 50% AIC model weight, included the amount of woodland in the 1 km buffer and the number of regenerating stems. The second model additionally included plant species richness and had an AIC weight of 30% (Table 5). These models both indicated that the predicted presence of eastern bettongs was likely to increase as each variable subsequently increased. The next model was separated from the candidate set by more than 4 AIC values, indicating little influence on bettong occupancy of predator detections or other factors of landscape disturbance and environmental characteristics.

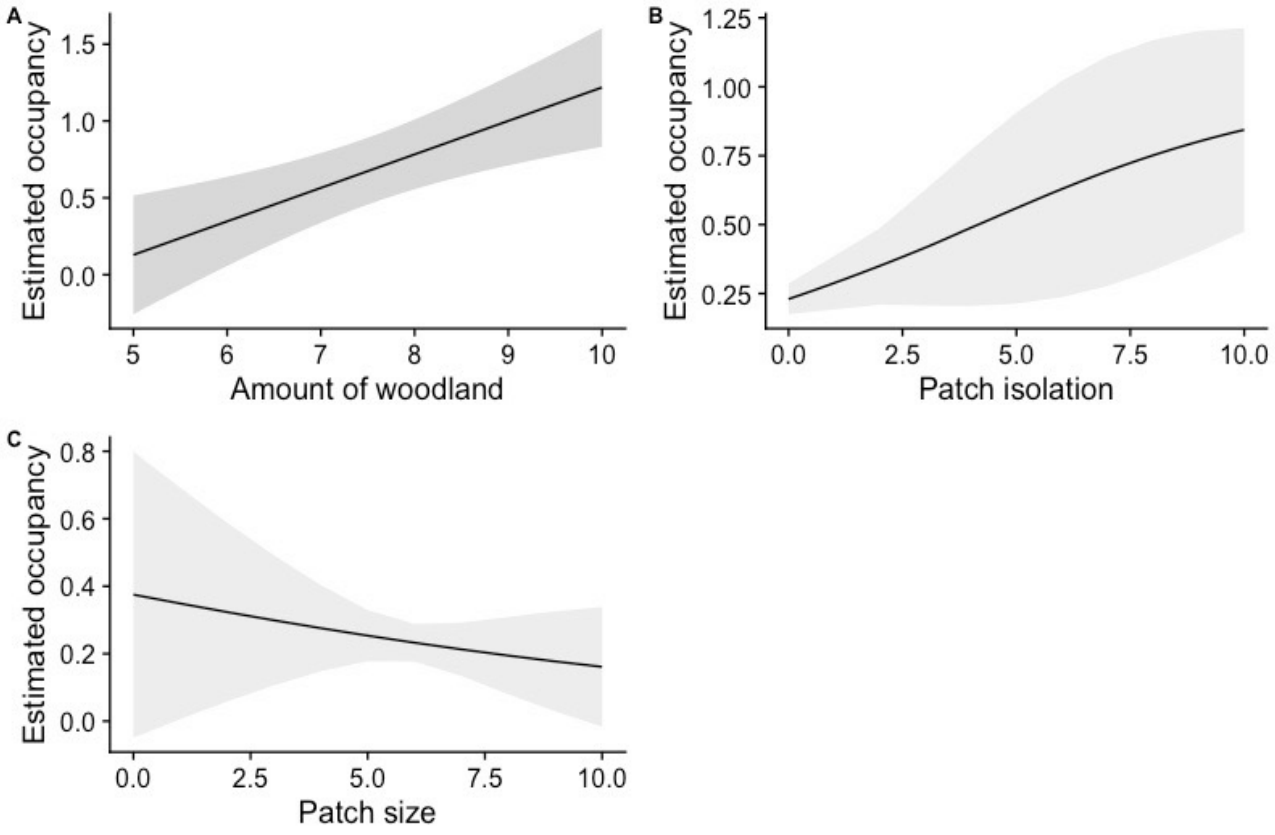

Figure 2. Estimated occupancy of eastern bettongs in a fragmented landscape considering A) Amount of woodland within a 1km buffer, B) Patch isolation (distance to nearest patch in km^2 and C) Patch size in km^2

Model	K	AIC	ΔAIC	AICwt
Woodland+Regen	7	270.95	0	0.51423
Woodland+Regen+Plant.richness	8	272.01	1.06	0.30266
Woodland+Quoll	7	275.65	4.7	0.04908
Woodland+Quoll+Cat	8	277.12	6.17	0.02353
Woodland+Distrd	7	277.98	7.03	0.0153
Woodland	6	279.23	8.28	0.00818
Woodland+Shrub	7	279.28	8.33	0.00798
Woodland+Mid+Shrub	8	279.49	8.54	0.00717
Woodland+Plant.richness	7	279.68	8.73	0.00654
Woodland+Distw	7	279.69	8.74	0.0065
Woodland+Mid	7	279.7	8.75	0.00646
Woodland+Over	7	280.99	10.04	0.0034
Woodland+Over+Shrub	8	281.14	10.2	0.00314
Woodland+Vvs	7	281.2	10.25	0.00306
Woodland+Cat	7	281.2	10.26	0.00305
Woodland+Over+Mid	8	281.68	10.73	0.00241
Woodland+Distw+Distedge+Distrd	10	281.72	10.77	0.00235
Woodland+Over+Mid+Shrub	10	283.33	12.38	0.00105
Null	5	285.72	14.77	0.00032
Isolation	6	286.69	15.74	0.0002
Agriculture	6	286.75	15.8	0.00019
Grassland	6	287.03	16.08	0.00017
Plantation	6	287.22	16.27	0.00015
Patch size	6	287.58	16.63	0.00013
Urban	6	287.72	16.77	0.00012
Patch size+Isolation	7	288.47	17.54	0.00011

Table 5. Candidate models used to determine best predictors of occupancy including bait age as a detection covariate, for eastern bettongs in a fragmented landscape in the Midlands, Tasmania.

2.5 Discussion

I tested whether the occupancy of a dietary and habitat specialist, the eastern bettong, was better explained by the amount of habitat in the landscape (habitat amount hypothesis) or the configuration of patches of habitat (island biogeography and metapopulation theory). Bettongs do not explicitly occupy the agricultural matrix, but only use it to traverse between patches and so did not explicitly test the habitat continuum hypothesis (which assumes all habitat types can be occupied). The key result of our study showed bettong occupancy to be strongly predicted by the amount of woodland habitat within a radius comparable to the size of individual home ranges. This result suggests that eastern bettongs respond to landscape alteration by incorporating sufficient habitat into their home range, even if they have to move across pasture to reach

several patches of woodland. Our results are consistent with the habitat amount hypothesis of species' response to landscape fragmentation. I did not find any effect on bettong occupancy of the size of patches of woodland or the degree of isolation of remnant patches independent of habitat amount, indicating that the classical theory of island biogeography (or metapopulation ecology) was not useful in predicting the effects of habitat loss on this species in this region. I also found that a measure of habitat quality – stem density, indicating both the ongoing tree regeneration in woodland patches and availability of food for bettongs – was a useful predictor of habitat quality. That is, in this disturbed and fragmented habitat, small and isolated patches of remnant woodland are valuable in supporting the persistence of the eastern bettong provided those patches remain in good condition.

Habitat fragmentation will affect species differently due to their different dietary requirements and movement patterns. Generalists have a broader niche breadth, and are more likely to persist in modified landscapes, while specialists or species in high trophic positions and rarer species are more at risk of local extinction (Martinson & Fagan 2014; Doherty & Driscoll 2018a). Patterns of patch-occupation of species will also differ according to their movement capacity. Low innate movement capacity can result in species being isolated to a patch, and therefore more likely to be influenced by habitat patch size and isolation. This could explain why some studies that have found stronger effects of patch size and isolation have been of plants and arthropods (Bullock *et al.* 2002; Ghazoul 2005; Evju & Sverdrup-Thygeson 2016; Haddad *et al.* 2017). Larger ranging species are more able to reach multiple patches of habitat within a landscape to find the resources they need (Gastón *et al.* 2016; Fattebert *et al.* 2017). The eastern bettong, while a woodland specialist species, is a mobile animal in which individuals have relatively large ranges for their size. GPS-tracking of eastern bettongs in this study area shows that bettong's can occasionally cross small gaps between remnant woodland patches (Gardiner et al. *in review)*. The classic metapopulation theory is therefore less applicable to species with movement patterns extending beyond single patches.

Each of the hypotheses considered in this study depicts the importance of fragmentation at different spatial scales. At one extreme, the metapopulation and island biogeography theory categorises landscapes into 'habitat' and 'non-habitat', disregarding the ability of individual species to use the spaces between habitat patches. On the other hand, the habitat continuum hypothesis suggests that all habitats are used by individual species, albeit at different intensities. Because landscapes are heterogeneous, no one hypothesis is

likely to be applicable to all regions or species, as is evident from the varying support for each hypothesis in the literature. Also, as many of the different types of patterns of fragmentation are correlated (Evju & Sverdrup-Thygeson 2016), the habitat amount hypothesis can be considered as one component of a scale in measuring responses to habitat fragmentation. Hanski (2015) suggests the habitat amount hypothesis would be applicable only at small spatial scales and in regions that still retain much of their original habitat. Our results revealed a strong effect of habitat amount at large scales in an area that has lost most of its original woodland vegetation, in agreement with other large-scale studies (Melo *et al.* 2017; Seibold *et al.* 2017). The habitat amount hypothesis places importance on smaller fragments, which are often disregarded as being usable habitat. Our study indicates that smaller fragments can indeed make valuable contributions to the total amount of habitat accessible to a species. In such cases, the amount of available habitat can be achieved by restoring and or planting native vegetation around remnants. By removing the strict delineation of what is considered habitat, the habitat amount hypothesis can be an effective management tool in modified landscapes which still retain scattered remnants.

Habitat quality is a key factor in habitat selection, and therefore influences the presence of a species (Chandler & King 2011). The strongest indicator of woodland quality as habitat for bettongs was the total density of stems of over storey trees. High stem density indicates larger numbers of small stems, which in turn is an indication of continuing woodland regeneration and thus healthy woodland. Stem density also indicates availability of food for the eastern bettong. This species feeds mainly on the subterranean fruiting bodies of ectomycorrhizal (ECM) fungi (Johnson 1994c), and the abundance of bettongs in different habitats is positively related to mycorrhizal activity (Taylor 1992). ECM fungi are associated with the fine roots of trees and shrubs, especially with *Eucalyptus* and *Acacia*, which are the dominant canopy and mid-storey genera in our study area. Foraging activity of eastern bettongs is concentrated in areas where the density of stems is high, probably because this is related to higher biomass of fine roots, and therefore higher production of ECM fungi (Johnson 1994a). Apart from this effect of stem density, I found no relationships of vegetation cover or plant-species richness on the presence of bettongs.

Surprisingly, occupancy by eastern bettongs was not strongly related to detections of predators. Our camera study and current ongoing studies have recorded bettongs, feral cats and spotted-tailed quolls

frequently using the same woodland. The Midlands has the highest recorded density of feral cats in Australia and their occupancy in the Midlands is best predicted by edge habitats between remnant woodland and pasture or grassland (R. Hamer, unpubl. data). Spotted-tailed quolls use the interior of woodland remnants (R. Hamer, unpubl. data) and both spotted-tailed quolls and Tasmanian devils are significant predators of medium sized mammals (Jones & Barmuta 1998; Pemberton *et al.* 2008; Andersen *et al.* 2017) and would probably prey on bettongs in shared habitat. Devils are currently very scarce due to severe population decline from facial tumour disease (Lazenby *et al.* 2018) The Midlands landscape supports high densities of European rabbits (*Oryctolagus cuniculus*) which are common prey for spotted-tailed quolls on mainland Australia (Belcher, Nelson & Darrant 2007). It is possible that feral cats and spotted-tailed quolls focus on abundant alternative prey, including rabbits, black rats, and lizards. On the mainland of Australia, the eastern bettong has disappeared, primarily because of predation by red foxes (Woinarski, Risler & Kean 2004; Johnson 2006). The red foxes have not been detected since 2009 (Sarre *et al.* 2013) and are likely no longer present in Tasmania.

The occupancy of eastern bettongs was not influenced by distance to infrastructure or water bodies. This could be attributed to the configuration of these features within the landscape. Most roads and water bodies are adjacent to expanses of pasture and the lack of detections of bettongs in pasture meant that bettongs were not present in close proximity to these landscape features. Species can be influenced by abiotic factors such as climate and soil type, as these directly influence mycorrhizal productivity. However, it was unlikely these would be significant because there was not enough variation across the study site and within our study period.

The Midlands region of Tasmania is a National Biodiversity Hotspot and the focus of a restoration project to minimize and reverse the loss of biodiversity caused by the expansion of agriculture. Two large biodiversity corridors are being constructed across the Midlands to connect core the dry woodlands and forests from the Eastern Tiers to the Great Western Tiers (Jones & Davidson 2016a). Existing remnant patches are being restored by managing grazing and fire and corridors planted following riverine systems to link remnants and core habitat. In both restoration and plantings, the full complement of tree, shrub and understorey species are being restored. Our results indicate that bettongs are likely to respond positively to these efforts as the total amount of habitat increases, the remnants are better connected and thus more

accessible, and the regeneration (number of stems) improves habitat quality by increasing germination and survival of seedlings of the tree and understorey species which provide food for bettongs. I didn't detect bettongs in any of the 23 restoration sites that were part of this survey. This can be explained by the current distribution and age of restoration plots. The new plantings, that are part of the recent biodiversity corridor construction, are too young to provide useful habitat to bettongs. Older restoration plots on farms have usually been established in extensively cleared areas, where they provide ecosystem services such as shelter for livestock in very open parts of the landscape. These restoration plots are thus often surrounded by pasture and grazing paddocks and are at a significant distance from woodland habitat. As a woodland specialist that plays an important functional role in ecosystem health, potentially promoting plant germination in diggings (Eldridge *et al.* 2015) and dispersing the spores of ectomycorrhizal fungi which provides nutrients of trees in low fertility soils, the bettong could itself enhance the success of restoration and recovery of degraded areas.

2.6 Conclusion

Our study shows habitat amount to be a more useful predictor of patch occupancy than patch size and isolation in a habitat specialist that is also sufficiently mobile to move between habitat patches. When a species is able to move across unsuitable habitat such as pasture to reach multiple patches, all remnants including smaller fragments contribute to the total amount of habitat available to the species. Habitat quality is also important, and the use of these large and small remnants is increased as their quality improves. Where the species has disappeared due to the extent of habitat loss, increasing the amount of habitat and improving the quality of the remnants could be effective strategies for their persistence. Future work combining movement ecology and landscape ecology could further our understanding of the effective scale of management needed.

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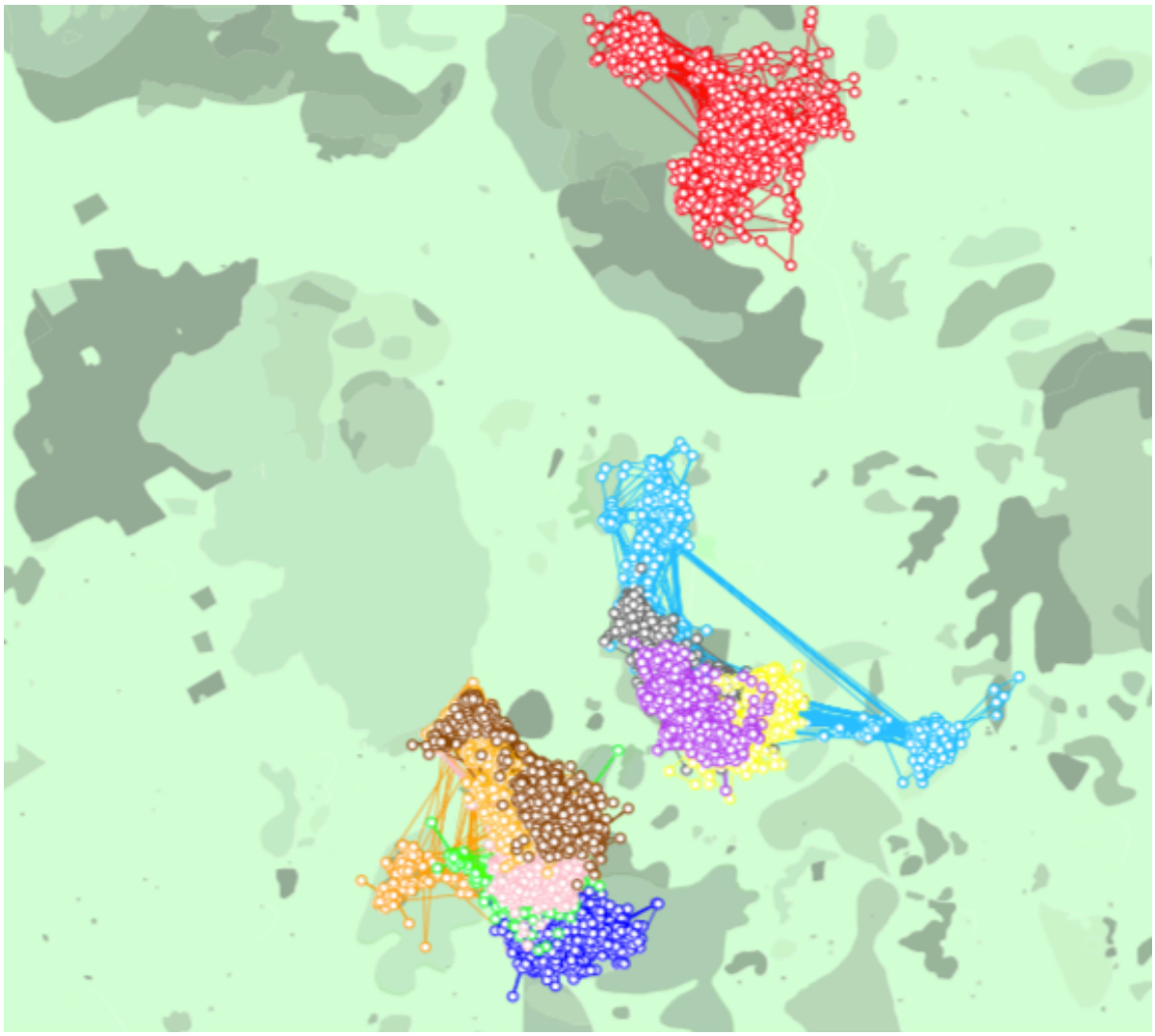
Chapter 3: Habitat quality is more important than configuration for a mobile woodland specialist



Raw bettong tracks in the Midlands

1.1 Abstract

Habitat fragmentation is a global challenge for biodiversity conservation. Studies of impacts of fragmentation have focused heavily on measures of species presence or absence in fragments, or species richness in relation to fragmentation, but have often not considered the effects of fragmentation on ranging behaviour of individual species. Effective management will benefit from knowledge of the effects of fragmentation on space-use by species. I investigated how a woodland specialist, the eastern bettong (*Bettongia gaimardi*) responded to fragmentation in an agricultural dominated landscape, the Midlands bioregion. I tested whether individual eastern bettongs could adjust home-range size to maintain access to essential habitat across three sites differing in degree of fragmentation. I used GPS-tracking to measure the home ranges of individual bettongs. Our models tested the effects on individual home range of habitat fragmentation, habitat quality and habitat amount, as measured at two scales: within a radius comparable to a typical core range (250 m radius) and a typical home range (750 m radius). I also estimated population density at each study site and included effects of density in our models.

Our results show that habitat quality, amount of woodland and population density were the most important determinants of home ranges of eastern bettongs. Home ranges were smaller when woodland quality was higher, and bettongs respond to increased woodland amount by occupying larger ranges. Individuals restrict their ranges in areas of higher quality but can increase their ranges if there is enough woodland. Moreover, increased density is expected to increase home range size, however large variations in density across our sites suggest this is limited by habitat area. This study has important implications for management. Species that are relatively mobile, can cross the matrix and utilise multiple patches may be able to compensate for the effects of habitat fragmentation by increasing home-range size. Instead I show all patch sizes are of value within a home range and therefore I propose management efforts should focus on improving habitat quality. Moreover, a baseline of population density within a fragmented landscape can improve management decisions, by providing an indication of population persistence in relation to habitat area and therefore target areas at risk of local extinction and promote connectivity.

1.2 Introduction

Habitat fragmentation is a global threat to biodiversity, and a challenge for conservation managers (Haddad *et al.* 2015; Hanski 2015). The fragmentation of continuous habitat into isolated patches can constrain species distributions and threaten population viability by reducing local population size (Fahrig 2017). Whether species can persist in fragmented landscapes depends largely on the ability of individuals to meet their resource requirements, but this is rarely tested. As habitat fragmentation becomes more widespread (Lindenmayer & Fischer 2007; Haddad *et al.* 2015; Tilman *et al.* 2017), management of the habitat that remains in fragmented landscapes will be increasingly important. Such management should be grounded in a detailed understanding of how use of space responds to fragmentation.

The impacts of habitat fragmentation on wildlife species have generally been described in terms of how landscape configuration influences species richness in fragmented landscapes, or the presence of individual species in fragments. Effects of fragmentation on these variables are often interpreted in relation to classic metapopulation and island biogeography theories, or more recent ideas such as the habitat continuum and amount hypotheses (Fischer, Lindenmayer & Kaitala 2006; Fahrig 2013; Hanski 2015; Lindgren & Cousins 2017). However, these broad approaches do not take into account the behavioural responses of individual species to habitat fragmentation, which are crucial in determining whether they are able to persist in fragmented landscapes.

Species-specific responses to landscape heterogeneity and fragmentation can be understood from studies of individual movements, which reveal individual and population-level requirements for habitat area and show how animals meet those requirements. Home ranges incorporate all movements and so provide a useful metric to identify variation in use of space. There has been a great deal of research on variation in home-range size as a function of body size, diet and, more recently, habitat modification (Beasley & Rhodes 2010; Tucker *et al.* 2018). Still, there is little information on the extent to which animals can adjust home-range area to meet their habitat requirements in fragmented landscapes. Species that can adjust their ranges to incorporate adequate habitat are less likely to be threatened by fragmentation than species that are restricted to small patches by unsuitability of the surrounding matrix in fragmented landscapes. For species

thus confined, competition for resources within small patches is likely to be high and population density should be correspondingly reduced, potentially compromising population viability (Beest *et al.* 2014). Moreover, fragmentation is often accompanied by degradation of habitat quality which can render patches unusable lacking in the resources to support viable populations (Fischer & Lindenmayer 2007b).

Here, I investigate how home ranges of the eastern bettong (*Bettongia gaimardi*) are affected by fragmentation of its woodland habitat. The eastern bettong is a small (~1.5kg) member of the marsupial Family Potoroidae and is a woodland specialist. It is distributed over the drier eastern half of Tasmania and occurs both in intact and highly fragmented woodland. The majority of the remaining wild population of bettongs falls within the fragmented Midlands bioregion on the island state of Tasmania. Occupancy of bettongs in this region is predicted by the quality and amount of habitat within a home-range radius of a camera site (Gardiner *et al.* 2018)

Our specific aim is to determine how fragmentation influences species persistence, by measuring its influence on individual home ranges. I predict that if bettongs can compensate for fragmentation through increased movement, their home range size would increase in fragmented areas as they expand their range of movement to find essential habitat resources. However, limitations on the ability to move among patches would be reflected by a reduction in home-range area with increasing fragmentation, as individuals become confined to one or a small number of habitat patches. I also incorporate estimates of habitat quality and population density as these are often altered by fragmentation. I expect individuals to concentrate their movement around higher quality patches, but their ranges are likely to increase with increasing density, as competition for resources increases in limited space.

3.3 Materials and Methods

3.3.1 Study site

The Midlands region of Tasmania, Australia, is a national biodiversity hotspot (https://www.environment.gov.au/biodiversity/conservation/hotspots/national-biodiversity-hotspots,

accessed 24/05/2018) covering an area of approximately 7760km^2. In the 200 years since European settlement of the region, the landscape has undergone extensive habitat conversion to support agricultural expansion for livestock production and crops. Less than 10% of the original woodland and less than 3% of original native grassland remains (Jones & Davidson 2016a). The remaining habitat varies in degree of fragmentation and is further threatened by inappropriate fire management and grazing pressure. The Midlands receives approximately 500mm of rainfall annually, with yearly temperatures ranging between -4 degrees to 32 degrees Celsius. Sites were selected opportunistically using results from a landscape-scale camera survey (Gardiner et al. *in review*) with the aim of including sites with a range of different degrees of fragmentation. Three agricultural sites of different degrees of fragmentation were selected to trap and track the movements of eastern bettongs. An additional site, in continuous habitat in a formal reserve, was included to trap and estimate population densities (Figure 1).

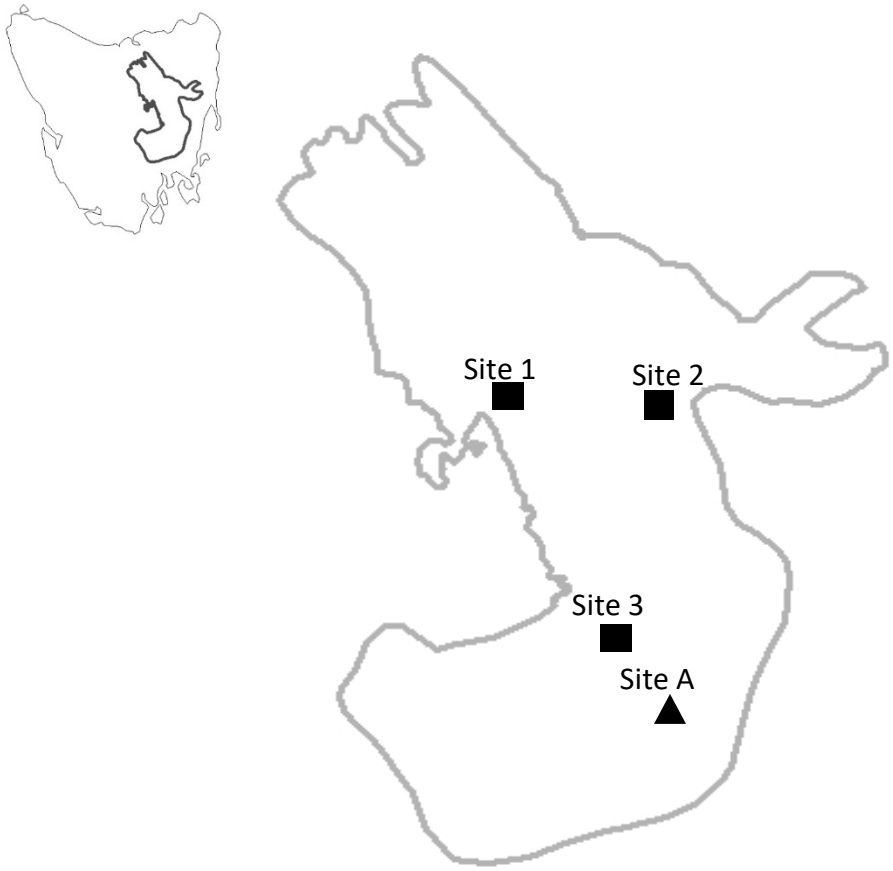


Fig 1. Map showing our sites in the Midlands bioregion of Tasmania, Australia. Squares represent sites where density and home range estimates were calculated. The triangle (Site A) represents the protected reserve site which was used as a comparison for density estimates.

3.3.2 Trapping and tracking

Eastern bettongs were trapped between June 2015 and May 2017. Trapping sessions included 3-5 nights of trapping per week for 3 weeks at each site. 32 Wire cage traps (Mascot traps; 30 x 60cm) were set at each site before dusk along unsealed tracks at 150 m intervals and baited with a standard bait of peanut butter and rolled oats. Traps were checked within the 5 hours after sunset. Captured animals were permanently identified by subcutaneously inserting PIT tags. Bettongs were weighed and sexed. Individuals weighing more than 1 kg and deemed to be adults and not growing were fitted with collars mounted with a GPS logger (G10 UltraLITE GPS logger) and VHF transmitter (Advanced Telemetry Solutions, Australia). Collars were programmed to take fixes every 15 minutes between 1800 and 0600 hours while animals were active. Collars were retrieved one month after deployment. All GPS locations collected during the night that an individual was fitted with a collar and during the night the collar was removed were excluded in analyses of home range to prevent bias resulting from trapping and handling disturbance. A total of 26 individual bettongs (14 males, 12 females) across the three fragmented sites were tracked within this study (Table 1).

3.3.3 Density

To understand how fragmentation affects population density, I estimated density at four different sites (Figure 1): a protected reserve with a large area of intact woodland habitat (Site A) and three fragmented agricultural sites (Sites 1 - 3). Density of eastern bettongs was estimated using spatially explicit capture-recapture (SECR) methods from trapping data (Borchers & Efford 2008), implemented in the 'secr' package (Efford 2012) in R 3.2.1. The SECR method assumes that the probability of detecting an individual is highest at its activity centre and radially decreases with distance. I assigned a half normal detection function with a pre-determined buffer of 3000m (double the width of an average bettong's home range) for the distance representing a zero-detection probability. Site and sex were included as single and combinations of covariates in models and compared to the null model. I did not include a trap or bait covariate as these were kept constant across sites and trapping sessions. Models were fit using maximum likelihood and ranked using AIC criterion (Burnham & Anderson 2002), (Table 2). Density estimates were then calculated per habitat area

(area of woodland) at each site. These density estimates were incorporated as a variable in the home-range analysis.

3.3.4 Utilisation Distribution estimates

I calculated utilisation distributions (UD) using Brownian bridge kernels (Horne *et al.* 2007). This method assumes successive relocations are not independent but instead are time dependent. The parameters used include relocations, the distance between relocations, and the Brownian motion variance (the animal's speed between successive locations). This method can generate home range sizes from movement paths, while also including pathways between points, which may be ignored in traditional kernel and MCP analysis (Walter *et al.* 2011). Estimates were obtained using the 'kernelbb' function in the adehabitatHR and adehabitatLT packages (Calenge & Calenge 2017) in R version 3.2.1. The UD was calculated for each individual at the 95% isopleth.

3.3.5 Landscape measurements

To standardise landscape measurements, I calculated the point of mean activity for each GPS-tracked animal by averaging all recorded locations. Buffers were placed around each mean centre to represent the area that could be used by that bettong. A buffer of 250m radius represented the core daily active areas within a home range, and the 750m radius encompassed the total home range area of both sexes. Buffers were overlayed on vegetation maps using TASVEG 3.0 layers provided by TASVEG LIST (http://dpipwe.tas.gov.au/conservation/development-planning-conservation-assessment/planning-tools/monitoring-and-mapping-tasmanias-vegetation-(tasveg)/tasveg-the-digital-vegetation-map-of-tasmania). Vegetation community classifications were combined to three basic types: woodland, pasture, and plantations. The amount of each habitat type was quantified within each buffer, as well as the 'perimeter: area' ratio of woodland to non-habitat as a fragmentation index (Ewers & Didham 2006).

Previous studies have suggested that stem density, which indicates regeneration of over-storey vegetation, is an indicator of woodland health and habitat quality for eastern bettongs (Gardiner *et al.* 2018). Higher density of stems suggests a larger biomass of fine roots on which mycorrhizal fungi grow, producing the fruit-bodies ('truffles') that are the main food for bettongs. Therefore I incorporated stem density as a measure of quality. At each site I placed 2 x 50m transects, intersecting each other at the centre and running in each cardinal direction. Stem density was calculated by counting the number of regenerating stems of over-storey eucalyptus tree species within 5 meters either side of the transect. The total counts were averaged across each site and the density per hectare used as a variable for habitat quality at each buffer size.

3.3.6 Statistical analyses

To determine the processes driving variation in home range size, I used generalised linear models. Home range size was used as the response variable in all analyses. Explanatory variables included habitat amount, fragmentation index, habitat quality and bettong density at a site (Table 1). Collinearity of variables was tested using Pearson's correlation and variance inflation factors. Variables with a variance inflation factor of more than 3 suggests severe collinearity (Zuur, Ieno & Elphick 2010). The amount of fragmentation and habitat quality were highly correlated and were therefore never tested in the same model. I expected sex to play a significant role in the variance of home range size and therefore included sex as a parameter in all models. Models were built including all possible combinations of explanatory variables. Multi-model inference (Burnham & Anderson 2002) was used to determine the models that best described the parameters influencing bettongs home range size in response to fragmentation; models were ranked using Akaike's Information Criterion with package AICModAvg. The final candidate model set included those models within 2 AIC values of the lowest AIC value.

Variable	Definition
Density	Density of bettongs per habitat area calculated using SECR analysis
Wood250	Amount of woodland within a 250m radii of the mean centre
Wood750	Amount of woodland within a 750m radii of the mean centre
Frag250	The ratio of perimeter:area of woodland within 250m radii of the mean centre
Frag750	The ratio of perimeter:area of woodland within 750m radii of the mean centre
Regen250	Stem density per hectare of overstorey species within 250m radii of the mean centre
Regen750	Stem density per hectare of overstorey species within 750m radii of the mean centre

Table: 1 Variables used in general linear models to explain home range variations of Eastern bettongs in the Midlands bioregion of Tasmania, Australia.

3.4 Results

Over a total of 305 trapping nights (occasions), there was a total of 169 captures of bettongs with 84 spatial recaptures over the 4 sites chosen to estimate density (Supplementary 1). Our spatially-explicit capture-recapture analysis showed that bettong density varied across 4 sites, within 3 fragmented and one conservation area (Table 3; Supplementary 2). The best model suggested there was no effect of sex on detection probability, but this did vary between sites (Table 2). The protected reserve site (Site A) was estimated to have approximately 10 times more bettongs per habitat area than the site with the least amount of woodland (Site 1, Table 3). Bettong density increased with increasing amount of woodland habitat in an area, suggesting that population size can be limited by fragmentation.

Model	Covariates	K	logLik	AIC	AICcwt
1	Site	7	-488.574	991.148	1
2	Site + Sex	8	-513.9402	1043.88	0
3	Sex	7	-515.7259	1045.452	0

Table 2. Candidate models used to estimate density using spatially explicit capture recapture for bettongs at 4 sites in the Midlands region of Tasmania

Home ranges of eastern bettong included an average of 80% woodland, 10% plantation, 9% pasture and 1% grassland. I observed large variation in home range size among individuals, sexes and sites. Males had larger home ranges than females ($F_{1, 2}$= 4.54, p= 0.04), with the model parameter estimates indicating about 40ha and up to 90ha larger (Table 4) with sizes ranging between 87-149 ha in males and 58-95 ha in females (Table 3).

Site	Woodland area (ha)	Male HR range size	Female Hr size	Density/ha
1	85	87.19 ± 26.4	58.37 ± 6.52	0.005 ± 0.0003
2	1291	149.07 ± 31.0	95.80 ± 18.15	0.008 ± 0.0003
3	157	113.1 ± 34.6	79.4 ± 2.87	0.02± 0.008
A	2301	-	-	0.05 ± 0.0008

Table 3: Summary of home range size (ha), density per habitat area (ha) and their standard error, of Eastern bettongs within the Midlands bioregion in Tasmania, Australia. Site 1-3 are the agricultural sites I tracked bettongs, site A is the protected reserve site.

There were five competing models in the final candidate set of models explaining size variation in bettong home range within fragmented landscapes, of which the two top models were equivalent in AIC value and weight (Table 4). These two models included sex (in all models), bettong density, and habitat quality (Regen) at either 250m or 750m radii buffer (ranked equivalent). Three further models in the final candidate set all had AIC weights of about 0.1. These models each included different variables: bettong density and the amount of woodland at 750m, habitat quality (Regen or stem density) at 250m and 750m scales, respectively. The relative importance of the different variables tested for their influence on home range size was weighted towards habitat quality and secondarily bettong population density (relative importance of sex was one, but sex was deliberately included in every model). Habitat quality at both scales was the most important variable, with a total model weight across all models run of more than 70%. The amount of fragmentation within the sampled radii had little influence on home range size in bettongs, not appearing in any models in the final set.

Model	AIC	ΔAIC	AICw	sex	density	Regen250	Regen750	Wood750
1	248.0968	0	0.23	90.9 ± 12.7	21.6 ± 10.2	-0.4 ± 0.2	-	-
2	248.0968	0	0.23	38.7 ± 10.1	20.9 ± 10.1	-	-1.1 ± 0.3	-
3	249.7166	1.62	0.1	37.3 ± 10.4	20.7 ± 10.5	-	-	0.1 ± 0.03
4	250.7519	1.56	0.1	39.9 ± 10.8	-	-0.8 ± 0.3	-	-
5	250.9442	1.75	0.09	39.9 ± 10.8	-	-	-0.3 ± 0.1	-
Relative importance of variable				1.00	0.57	0.77	0.71	0.31

Table 4: Final model set describing the demographic and vegetation parameters that influence home range size of eastern bettongs. Density = bettong density; Regen250 = Stem density per hectare of overstorey species within 250m radii of the mean centre; Regen750 = Stem density per hectare of overstorey species within 750m radii of the mean centre; Wood750= Amount of woodland within a 750m radii of the mean centre. I report the estimate and standard error of parameters in each model, and their relative importance.

Home range sizes increased with increasing density. Parameter estimates indicated that home range size increased by about 21 ha for every increment increase in density, equivalent to an additional bettong per hectare (Table 4). On the other hand, home ranges decreased with increasing quality. Home range size decreased slightly (-0.8 ha at 250 m and -1.1 at 750 m) with each incremental increase (1.6 stems per hectare) in regenerating woodland tree stems recorded on the transect. Bettongs responded to the amount of woodland at larger scales (750 m) by slightly increasing home range size (+0.1 ha) with each 0.015ha increment in woodland.

3.7 Discussion

I tested species response to fragmentation in the eastern bettong, a medium-sized marsupial potoroid that is a woodland specialist, by investigating the processes that might cause variation in home-range size in fragmented landscapes. Our results suggest that habitat quality (as measured by the number of regenerating stems) and habitat amount have larger influences on home-range than habitat configuration. That is, individuals are able to meet their habitat requirements in fragmented landscapes by increasing their home range size. Habitat quality and habitat amount also influence occupancy (Gardiner *et al.* 2018). These results have important implications for habitat management, suggesting that the quality and amount of habitat, regardless of configuration, is most important for the persistence of this species.

Habitat degradation is a consequence of the process of habitat fragmentation, both directly and also indirectly as smaller fragments have greater edge effects, in which other impacts such as fire and grazing can affect a higher proportion of the patch. The effects of degradation, however, are frequently considered secondary to fragmentation. A review by Doherty and Driscoll (2018b) suggested that quality may be more important than landscape structure for emigration and immigration. Here I show that quality is also important for daily movements that together comprise home range. Low-quality habitat can influence daily behaviours of individuals, opposing fitness costs whereby they may have access to lower quality resources, but have to spend more time and energy acquiring them. Moreover, degradation is detrimental when patches become ecological traps (Taylor 2017). An ecological trap occurs when patches can be used but may not have adequate resources to support a resident or breeding population. This highlights why measuring presence or species richness may not be adequate to determine whether populations of a species can persist in an area. Habitat degradation is amplified by secondary threats such as grazing and the spread of alien plant species. Notably, our three trapping sites had either all or part of the woodland under covenant protection, where habitats cannot be modified by human activity, which may allow sites to retain some of their quality and have a buffer of protection. Managing anthropogenic threats (i.e. improper fire regimes, spread of invasive pasture and grazing pressures) and placing native remnants under some form of protection would be beneficial for landscape conservation.

Requirements for habitat area are species-specific, reflecting the particular resource requirements and movement capacity of individual species. Despite being a specialist, the eastern bettong has a relatively large home range for its body size, and as this study shows, it is able to increase its home range area to include additional habitat in response to fragmentation. This is congruent with the observation that species that have higher mobility are able to accommodate their habitat area requirements via movement (Anderson *et al.* 2005; Saïd & Servanty 2005; Martin & Fahrig 2016). In this case, patch size and isolation within the home range do not necessarily restrict habitat use; rather, small and isolated patches are of value because they contribute to the habitat amount that each individual requires for a viable home range. In comparison, species with smaller ranging capability are more restricted by fragmentation (Ewers & Didham 2006). The ability to compensate is advantageous in fragmented landscapes, providing better outcomes for juvenile dispersal,

translocations and reintroductions. Moreover, within our study, eastern bettongs were using plantations of native tree species even when they had to cross roads from the woodland remnants to reach them. Native tree plantations are fast-growing and can provide usable habitat within fragmented landscapes to increase habitat area where patches of remnant habitat are small. Increasing habitat amount is a beneficial conservation strategy; adding native vegetation as corridors or to smaller patches to promote connectivity may improve species movement and decrease the amount of time spent searching for habitat and exposed to edges or the matrix.

Home-range size of eastern bettongs was strongly influenced by population density, as seen in many mammals (Beest *et al.* 2016; Malin *et al.* 2016). Density was significantly higher within the reserve site than the sampled fragmented sites. Given bettongs can increase their ranges to accommodate for fragmentation, the loss and degradation of quality is likely a more important driver of population density and viability than fragmentation *per se*. Previous studies have reported bettongs at higher densities where soil fertility is low (Taylor 1993a); in agricultural landscapes the surrounding pasture is heavily disturbed and homogenised by grazing and input of pesticides and fertilisers. The soil composition is ultimately altered, making it unsuitable for native plants to grow or persist (Bailey, Davidson & Close 2012; Collins & Fahrig 2017) impacting mycorrhizal recruitment through a decrease in fine root biomass. The quality of patches will impact population viability, but should be further tested. Restoration efforts should implement frameworks to mitigate factors contributing to degradation including grazing pressures, fire management and soil quality. Moreover, acquiring baseline knowledge of density across a landscape is important to direct management and monitoring programs.

3.8 Conclusion

Our study shows habitat quality and area were the most important drivers for species home range size. For a mobile species which can utilise multiple patches, fragmentation may not have as much impact on habitat requirements, but can influence the quality of remnants. Our results agree with the review by Hodgson *et al.* (2011), which states that higher area and higher quality habitats are the most important factors determining species persistence, and should be a focus for conservation. This study has important implications for

management actions such as habitat restoration. Planting vegetation to improve structure or adding habitat with the assumption animals will subsequently colonise it may not sufficiently improve quality leading to animals not being able to use these areas. Future studies should incorporate experimental designs to better conceptualise patch quality for management purposes. Identifying where patches are degraded and subsequently investing in improving their quality can be important for species persistence and facilitated by combining movement and landscape ecology.

3.9 Supplementary

	Total captures	M	F	Occasions
Site1	47	8	8	11
Site2	50	5	5	21
Site3	19	7	9	11
Site A	53	24	18	9
Total	169	44	40	52

Supplementary **1:** Summary of trapping used to estimate density including total number of captures at each site, for each sex and the number of occasions (trapping nights)

	beta	SE.beta	lcl	ucl
D. Site 1	-3.11	0.34	-3.77	-2.44
D.site 2	-3.04	0.47	-3.96	-2.11
D.site 3	-1.39	0.44	-2.25	-0.52
D.site A	-3.00	0.16	-3.32	-2.68
Lambda	-2.45	0.02	-2.50	-2.41
sigma. Site 1	5.72	0.14	5.44	6.00
sigma.site 2	1.57	0.20	1.18	1.96
sigma.site3	0.83	0.14	0.55	1.11
sigma.siteA	5.83	0.00	5.82	5.84

Supplementary 2: coefficients and their standard error and 95% confidence intervals (lower- lcl and upper- ucl) of each parameter for the top model measuring density using SECR analysis for each site. D= density estimate, Lambda=the exposure probability of each trap, sigma= the effect of sex on the scale factor of the home range.

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Chapter 4: State space modelling reveals habitat perception of a small terrestrial mammal in a fragmented landscape

Renet bouncing away after removing her GPS collar

4.1 Abstract

Habitat fragmentation is a major driver of species loss, and is expected to increase. Managing habitat for animal species has often been grounded in restoring or retaining vegetation, but this can fail if critical attributes are not present. Understanding an animal's perception of habitat can be an important tool for managing habitat effectively. A means to obtain this understanding is to study animal movements, so that key habitat attributes can be identified according to how individual animals move in relation to them. Movement is frequently generalised to describe a total area used, or segmented to highlight resource use, often overlooking finer-scale individual behaviours. I applied Hidden Markov Modelling (HMM) to tracking data from 24 eastern bettongs (*Bettongia gaimardi*) to identify movement-behaviour states and the habitat features associated with them at three sites in a fragmented and agriculturally-dominated landscape. I identified three distinct behavioural states, categorised as denning, foraging and fast travelling. Transitions between these states were explained by the sex of the individual, the density of vegetation and the extent of cover. Individual movements highlighted that bettongs were highly reliant on the presence of woodland, in which much of their movement was concentrated. Additionally, bettongs did move outside woodland patches, often fast travelling through pasture and using smaller stands of trees to move to neighbouring patches. Our results show that for mobile species such as the eastern bettong habitat fragmentation may not hinder movement, but can be facilitated by smaller patches of habitat. Use of habitat is reliant on retaining higher quality patches. Future work should focus on applying HMMs to even smaller and more habitat-restricted species to increase our understanding of habitat perception for a finer scale understanding to manage habitat more efficiently.

4.2 Introduction

Human activities have caused the loss and fragmentation of habitat, contributing to the global decline of biodiversity (Maxwell *et al.* 2016). Species in fragmented landscapes are increasingly being restricted to smaller and degraded areas of their natural habitat. Management of animals species threatened by habitat fragmentation often attempts to preserve or restore habitat by means of planting

native vegetation, with the assumption that the resultant structure is suitable for the animals. These efforts can fail if necessary habitat elements for the target species are not present (Palmer, Ambrose & Poff 1997; Peipoch *et al.* 2015). Understanding how a species interacts with its environment and thus which elements of the environment are perceived by the species as habitat (Jones & Davidson 2016b) is necessary to restore and enable persistence of wildlife in the landscape.

Combining movement and landscape information to obtain finer scale understanding of habitat state and species-habitat requirements (Allen & Singh 2016; McClintock *et al.* 2017; Browning *et al.* 2018) can be a powerful tool for directing management. Animal movement facilitates our understanding of how an animal perceives habitat. The patterns of movement reflect the decisions made across daily behaviours, and can reveal which elements of the environment a species values and uses (Nathan *et al.* 2008; Jones & Davidson 2016b), thus highlighting what elements need to be managed. With improved technology, it has become possible to acquire larger and more accurate data sets on the movements of individual animals. In particular, GPS tracking can provide highly resolved data on the movements of species that are otherwise difficult to observe (Tucker *et al.* 2018). Animal movement is often quantified by describing the total area and habitat features encompassed by a set of locations or segments of movement to determine area requirements and define effective scales of management. These studies include home-range analyses, first-passage time (McKenzie, Lewis & Merrill 2009), and resource-selection functions (Forester, Im & Rathouz 2009). While these approaches are useful, they do not exploit the potential of the finely-resolved data that can be provided by GPS tracking to identify explicit movement paths, and describe the spatial occurrence of behaviour states such as foraging and denning (Towner *et al.* 2016).

Movement paths of individual animals can be described as steps that are characterised by step lengths (representing speed of movement) and turning angles relative to the previous step. The density and distribution of speeds and angles in space can be used to infer behavioural states (Phillips *et al.* 2015).

For example, more tortuous angles and smaller steps usually indicate foraging, or occupation of preferred habitat. For example, using correlated random walks, Vernes and Haydon (2001) identified area restricted searching (i.e. foraging) by norther bettongs (*Bettongia tropics)* after a fire. On the other hand, longer steps and smaller angles can indicate transit through less favourable habitat (Maciel *et al.* 2013; Osbourn, Connette & Semlitsch 2014). Transitions between behaviour states are also important in identifying the external factors that affect movement, thus revealing the animal's perspective of its habitat.

Hidden Markov Models (HMM) provide a means to use sequential location data to infer distinct individual behaviour states and to describe the spatial and temporal pattern of switching between behaviour states (Patterson *et al.* 2008; Langrock *et al.* 2012; Leos-Barajas *et al.* 2017). They assume a set of behaviours represented by movement are dependent on an unobserved state and can capture patterns found in movement data, which are translated as a proxy behavioural state. Their ability to manage autocorrelated, missing and large data sets make them attractive to ecologists. They have most often been applied to wide-ranging species, often in the marine environment (Franke *et al.* 2006; Hart *et al.* 2010; Towner *et al.* 2016). However, they have rarely been applied to smaller terrestrial species, mainly because of lack of data due to the cryptic nature of species or limitations on the capacity of tracking devices that can be fitted to small animals.

The eastern bettong (*Bettongia gaimardi*) is a member of the marsupial Family Potoroidae and weighs approximately 1.5kg. It is both a keystone species and ecosystem engineer because, like other potoroid marsupials, it disperses the spores of ectomycorrhizal fungi and modifies soil conditions as a result of digging for fungi, providing benefits for woodland health (Johnson 1996; Vernes & Pope 2001; Claridge 2002; Fleming *et al.* 2014a). Eastern bettongs were formally distributed across the eastern half of Australia, but mainland populations went extinct after the introduction of invasive predators. The remaining wild population of the eastern bettongs occurs in the eastern half of Tasmania. Much of the

woodland and forest habitat of the eastern bettong in this region has been extensively converted for agriculture, and woodland remnants are highly fragmented, especially in the intensively farmed bioregion of the Midlands which forms the core of the bettong's distribution. While the eastern bettong is a woodland specialist with large individual area requirements, it is able to persist in fragmented landscapes (at low population density) provided that a sufficient total area of habitat is available in the local landscape (Gardiner et al. *in review*). Persistence under these circumstances is strongly affected by the movement behaviour of individuals, which allow them to gain access to the habitat area that they require. Therefore, finer-scaled knowledge of movement behaviour is essential to our understanding of the response of this species to habitat fragmentation.

In this study I use Hidden Markov Models (HMMs) to analyse how individuals move in a landscape where their woodland habitat is fragmented by land clearance for agriculture. This is the first study to use HMMs to investigate the movement of a small mammal, specifically to assess its perception of fragmentation. I use HMMs to categorise behaviour states from movement data, and identify habitat attributes that influence transitions between behaviour states. The eastern bettong is a nocturnal species, building nests in which to den during the day, therefore I expect them to concentrate their denning in woodland with denser vegetation. Previous studies have shown that higher stem density increases their use of habitat (Gardiner *et al.* 2018) therefore I suggest that the species will likely forage in woodlands with higher stem density. Lastly, I predict that when vegetation cover is low or absent, such as in open pasture, bettongs are likely to travel faster and in a less tortuous manner as they are more likely to be exposed to predators. Thus, I tested whether the percent of woodland cover, vegetation density and distance to woodland edge influence behavioural transitions.

4.3 Methods

Animal ethics approval was obtained from the University of Tasmania (permit A14879) and the Department of Primary Industries, Parks, Water and Environment (permit: FA15118)

4.3.1 Study area

The Midlands covers 7760km^2 of the eastern central area of Tasmania, Australia. The region is moderately dry (annual rainfall is typically 450-500mm), with mean winter average temperature reaching 5 ^{o}C and summer averages of 20 ^{o}C. The region is a biodiversity hotspot hosting a number of species of endemic fauna and flora, including a suite of marsupials that have declined and are threatened or extinct outside Tasmania. The natural vegetation of the region is grassland and open woodland, but over the last 200 years much of the original vegetation has been converted to improved pasture or cropland, such that only 10% of the original woodland and 3% of the original grassland remains (Jones & Davidson 2016b). Most remnants of original habitat are on private or protected property, and are often fragmented by roads, grazing pasture or plantations.

I studied movements of eastern bettongs at three sites that differed in amount of remnant woodland cover and degree of fragmentation. Woodlands at each site are broadly described as dry sclerophyll woodland, dominated by *Eucalyptus amygdalina* as the overstorey species, *Acacia dealbata* in the midstorey and with a patchy distribution of *Lomandra longifolia* (mat rushes) and *Pteridium esculentum* (bracken fern) in the ground level layer. Previous studies described habitat quality and the amount of fragmentation at each site (see Gardiner et al. *in review*). Site 1 is the least fragmented, site 2 is moderately fragmented site 3 is the most fragmented (Figure 1). Site quality has previously been measured as stem density of regenerating overstorey species (Gardiner et al. *in review*). Of the three sites, site 1 is considered to be of lower quality than the more fragmented site 2 and 3 (Supplementary 1). I did not include the conservation area, Site A, in the analysis as this information was obtained opportunistically from a separate project analysing the population genetics of bettongs in that area.

4.3.2 Trapping and tracking

I trapped Eastern bettongs between March 2016 and May 2017 (Table 1). Trapping was carried out for 3-5 days a week for 3 weeks at each site. Traps were wire cage traps (Mascot Wire Works, Sydney), baited with balls of peanut butter and rolled oats, set along transects running through the middle of woodland patches at 150m intervals. Upon capture, each individual bettong was PIT-tagged for identification, sexed and weighed. Animals were collared if they weighed more than 1.5 kg, to ensure that only mature adults received collars. Each collar included a dual G10 UltraLITE GPS logger and VHF transmitter (Advanced Telemetry Solutions, Australia, error location) with an average accuracy of ± 20m. Collars were deployed for approximately one month on each individual. Eastern bettongs are nocturnal, denning during the day, therefore the GPS logger was set to record fixes every 15 minutes between 1600-0600 hours. Individuals from Site 1 were tracked in May- June 2016, Site 2 from March- April 2016 and Site 3 in April-May 2017. VHF tracking was carried out to ensure collars were still functioning, and still on the animal.

4.3.3 Site attributes

Using ArcGIS 10.5 I overlayed all GPS points and identified habitat types each point intersected at each site using government vegetation layers- TASVEG 3.0 (http://dpipwe.tas.gov.au/conservation/development-planning-conservation-assessment/planning-tools/monitoring-and-mapping-tasmanias-vegetation-(tasveg)/tasveg-the-digital-vegetation-map-of-tasmania). I then calculated the Euclidean distance of points to the edge of the closest woodland. I also extracted values of percent woodland cover from TERN Auscover forest layers (http://data.auscover.org.au/xwiki/bin/view/Product+pages/Persistent+Green-Vegetation+Fraction). I wanted to highlight differences in vegetation density (structure) particularly within woodland sites. Using package raster (Hijmans *et al.* 2017) in R I extracted infrared bands from Landsat 5 raster layers (https://landsat.usgs.gov/landsat-in-action). I highlighted differences in density of vegetation, by first

calculating values of the Normalised Difference Vegetation Index (NDVI). I then used unsupervised K means classifications on NDVI layers to quantify vegetation densities. The K- mean algorithm classifies pixels based on the distances from cluster means (Lu & Weng 2007), higher values indicating denser vegetation, lower values indicating open habitat to bare pasture. I compared the k-mean values to Google Earth imagery, as well as researchers' knowledge of the site, to verify values were representative.

4.3.4 Hidden Markov Modelling

Analysis of movement was carried out using moveHMM package (Michelot, Langrock & Patterson 2016) in R 3.2.1 on all bettong tracks. Since HMMs are time-series models, our data were formatted to represent each day's record for an animal as a single track. Non-recorded times were coded as NAs. HMM model parameters are estimated via maximum likelihood using forward algorithms (Patterson *et al.* 2009). I considered a variety of initial starting values and checked model fit for each set of starting values, and therefore are confident I found the appropriate global maximum likelihood. I used gamma distributions for step lengths and von Mises distributions for turning angles.

I then modelled state transition probabilities as a function of site attributes. Vegetation density and sex were transformed into categorical variables, in which dummy variables (K-1) are added to the data as the probability of being observed at that time, as described by Michelot, Langrock and Patterson (2016). Percent cover and distance to edge were considered numerical variables. Models were run with single variables and combinations of covariates, and ranked using the AIC criterion. To examine how covariates affect state switching I computed stationary distributions as described by Patterson *et al.* (2009), to provide the marginal probability of a state at a given covariate value. Finally, model goodness of fit was assessed by examining pseudo-residuals.

4.4 Results

I collected 26,156 locations from 26 individuals, including 14 males and 12 females at three sites (Table 1) with a mean number of 1084 observations for males and 998 for females. First, I examined how many states could explain the movement displayed by testing 2 and 3-state models. Choosing the appropriate number of states can be challenging (Pohle *et al.* 2017), as traditional use of AIC ranking will favour the model with more states, which was the case in this analysis. Using Pohle *et al.* (2017) suggestion for choosing the number of states, I inspected pseudo-residuals for models fit for 2 and 3 states, showing a better fit for 3 states. Moreover, the fitted gamma state dependent distributions showed three unique movement types, and an additional examination of the temporal structure of the data, it was visible there were three structures present (Table 2 and Figure 3).

State 1 was characterised by concentrated, very short step lengths and more high tortuous movement indicated by turning angles. State 2 was characterised by short step lengths and higher turning angles and state 3 by long, fast steps with straighter paths and strong directionality (Figure 1). I identify state 1 as denning given the similarity to stationary distributions. State 2 was identified as foraging and state 3 as fast travelling. The average step length in each state was 28m $\pm$ 0.17, 103m $\pm$ 0.6 and 268m $\pm$ 1.7 for denning, foraging and fast travelling respectively.

ID	number of locations	sex	site
andive	1809	m	3
baldur	550	m	2
beetroot	1124	m	3
bjorn	683	m	2
dot	766	f	1
durian	1388	m	3
edwina	913	f	1
egbert	873	m	1
floki	973	m	2
freya	159	f	2
lagartha	940	f	2
maud	656	f	1
olga	773	f	1
othello	776	m	1
parsnip	1585	m	3
percy	795	m	1
potato	1553	m	3
pumpkin	1151	f	3
raddish	1483	f	3
renet	588	m	1
sifa	697	f	2
sprout	1654	f	3
swede	1298	m	3
tomato	1183	m	3
turnip	1784	f	3

Table 1: Tracking of eastern bettongs at the three different sites in the Midlands bioregion of Tasmania, Australia. Each site differed in the size, configuration and quality of habitat, site 1 being low in fragmentation, site 2 medium and site 3 high fragmentation.

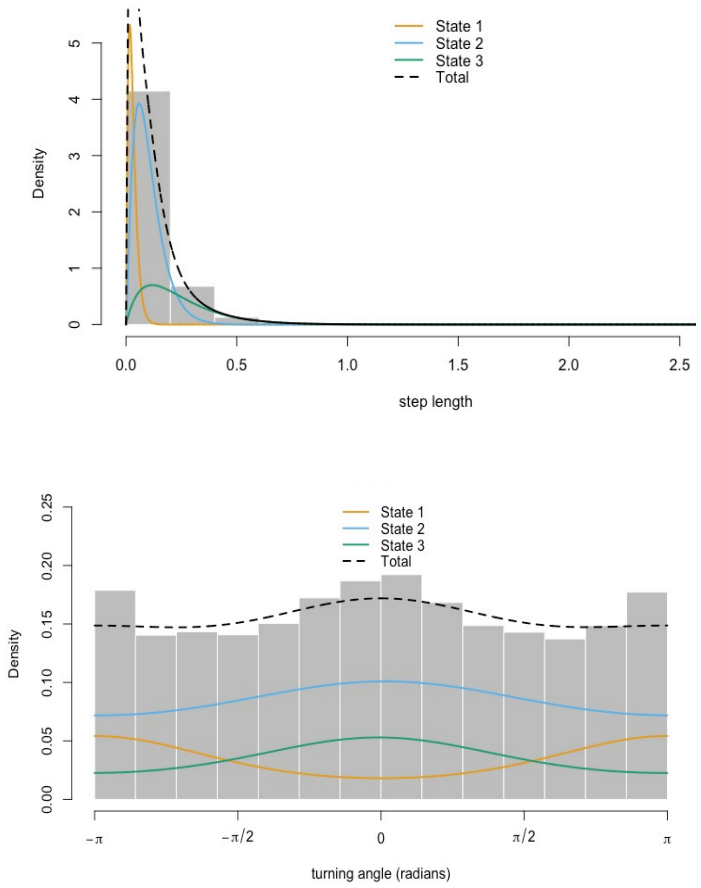

Figure 1 : Histogram depicting the density of step lengths and turning angle distributions derived from a 3-state model for all tracked individuals.

Overlaying tracks on site maps showed that individuals used woodland more than any other vegetation type. Denning was displayed as a clumped pattern occurring in areas of denser vegetation, foraging extended throughout woodland patches within the individual's range and fast travelling included fast paced movement between patches or more open areas (example Figure 2). Across sites there was a difference in the proportion of time spent in different states. All animals spent a higher proportion of their time foraging than in any other state: 53% ,72%, and 66% of locations were represented foraging at sites 1, 2 and 3 respectively. Fast-travelling made up 40%, 22%, and 15% of time at the three sites site. Denning made up 7%, 6% and 18%, occurring only towards the end or very beginning of the nightly tracking periods (Figure 3).

Model	AIC	Log likelihood
3-state	0	-10300.02
2-state	2442.44	-11531.24
VegIndex+cover+sex	0	-9842.499
Vegindex+sex	8.24	-9852.619
VegIndex+edge+sex	108.54	-9896.768
VegIndex+cover	266.89	-9981.944
VegIndex	267.88	-9988.439
cover+edge+sex	367.59	-10068.3
VegIndex+edge	367.78	-10032.39
sex+edge	469.28	-10125.14
sex+cover	481.15	-10131.07
Sex	591.45	-10192.22
cover	683.89	-10238.44
edge+cover	776.13	-10278.57
null	795.05	-10300.02
edge	991.22	-10392.11

Table 2: Likelihood and AIC values obtained from the Hidden Markov Models testing 1) feasibility of a 3-state model versus a 2-state model, 2) Habitat attributes tested to determine what drives transitions between states using a 3-state model.

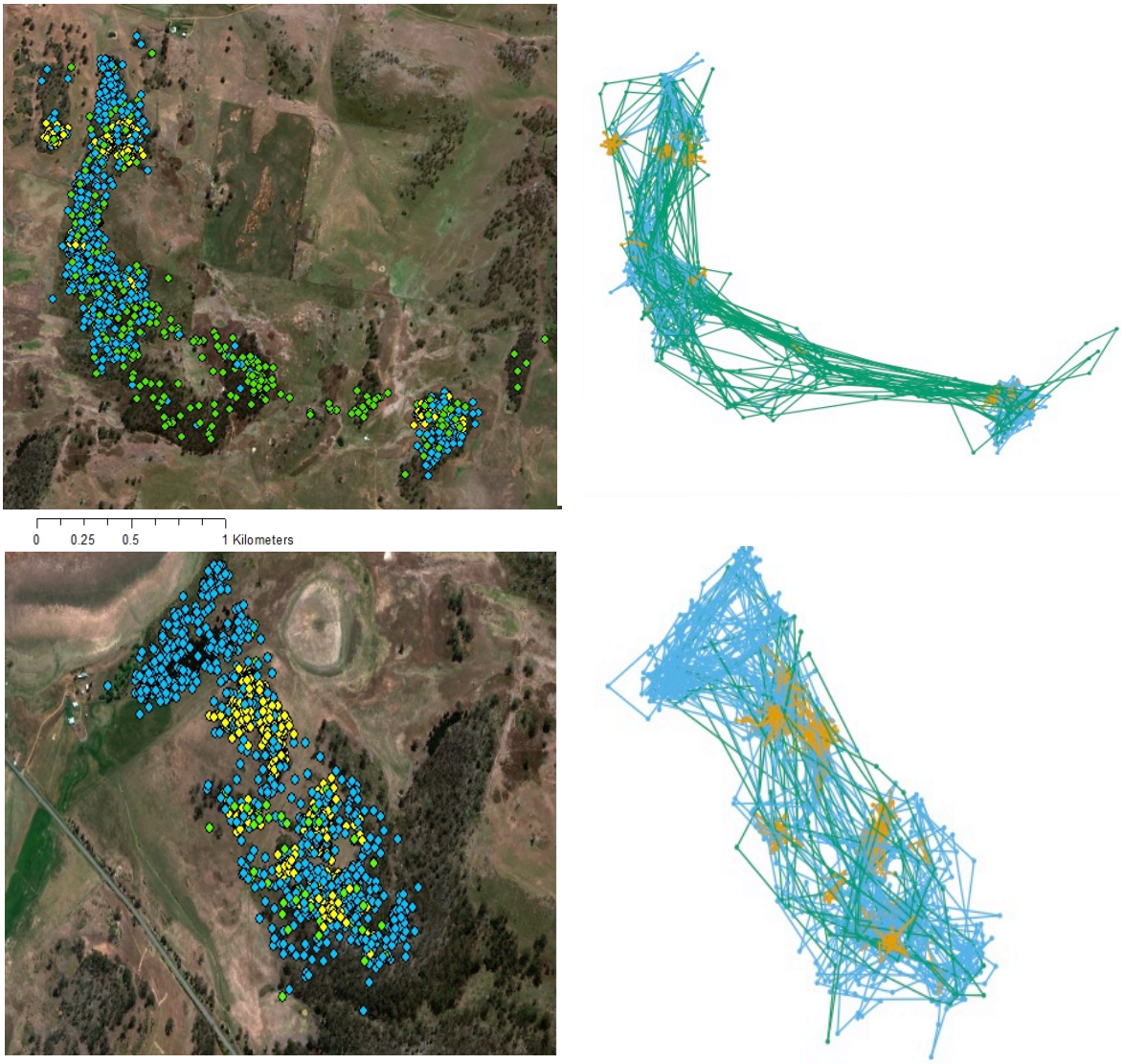

Figure 2: Example of tracks of a male (A) and female (B) bettong's locations, colour coded by their corresponding state. On the right is locations overlayed on Google imagery, on the left is the same tracks showing their overall movement. Yellow is denning (state 1), blue is foraging (state 2) and green is fast travelling (state 3).

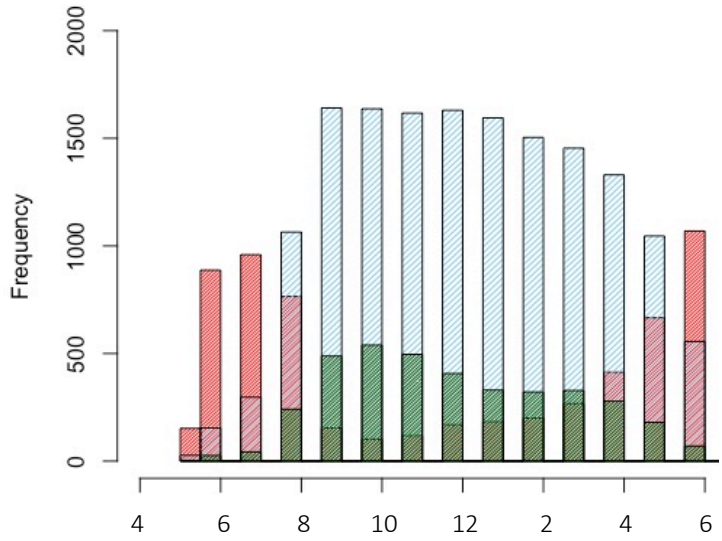

Figure 3: Frequency of states across time of active tracking between 4pm and 6am, each tick represent 2 hours. Red is State 1; Blue is state 2 and Green is state 3.

Our models testing site attributes as predictors of transitions between states suggested that vegetation density and woodland cover, along with sex, were the best predictors (Table 2). The marginal probability of bettongs denning was highest in mid to dense vegetation but lower woodland cover. Probability of foraging was highest in mid to high woodland cover but lower vegetation density. Fast travelling was most likely to occur in open to low vegetation density and woodland cover (Figure 4).

There was a decreasing probability of transitioning between denning to foraging, and travelling to foraging when vegetation density was high. This suggests bettongs den in more dense vegetation and forage or fast travel through less dense vegetation. If woodland cover was high there was a decreasing probability that bettongs would remain denning and/or transitioning between foraging to denning. Moreover, bettongs had higher likelihood of transitioning from denning to foraging and remain foraging

or fast-travelling with higher amount of woodland cover. This suggests bettongs will forage in higher woodland cover but move to lower woodland cover to den.

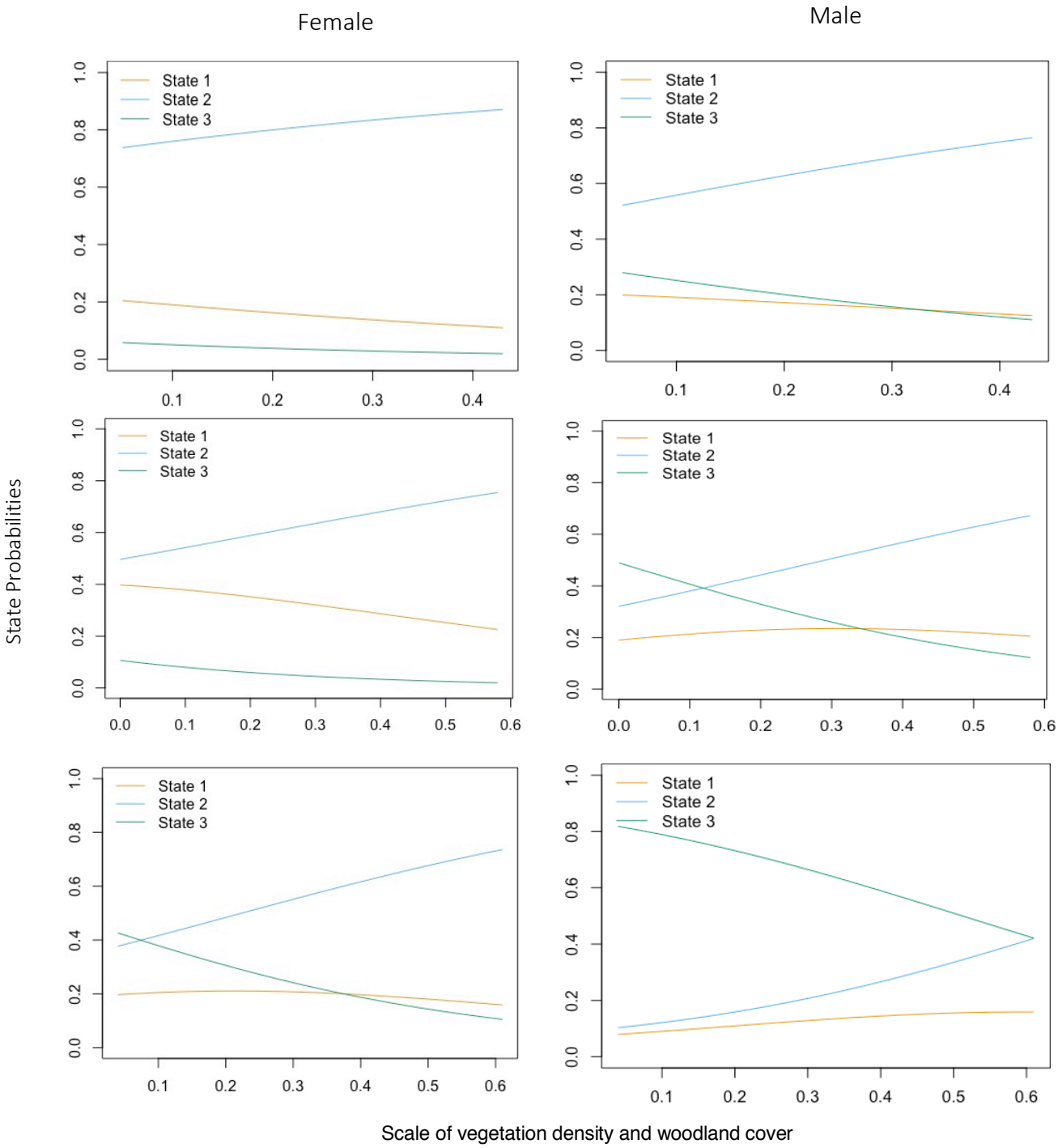

Figure 4: Example of stationary state probabilities of our best model for each sex. I show stationary probabilities for low (top), medium (middle) and high (bottom) vegetation density and woodland cover.

4.5 Discussion

Our study is the first to classify the behaviours of a small terrestrial vertebrate within a fragmented landscape using state-space models (Hidden Markov Models).I was able to use data on movement pathways to identify three behavioural states, and explain how sex and habitat features were associated with the occurrence of these behaviour states. Behaviours were interpreted as denning, foraging and fast travelling, and found that transitions between them were due to density of vegetation, sex and extent of woodland cover. The results provide insight into the decisions that animals make in relation to the characteristics of the landscape, in particular, their perception of the utility of the structure and configuration of vegetation.

The attributes of the local environment are important in influencing decisions made by animals on how they move through the landscape. The spatial occurrence of different behavioural states and the transitions between them in relation to local environmental features, provide insight into an animal's perception of habitat. The eastern bettong is a woodland specialist in which individuals have relatively large ranges. Previous studies exploring the responses of eastern bettongs to fragmentation and habitat characteristics highlighted the importance of habitat amount and quality in determining their occurrence (Gardiner *et al.* 2018) and the structure of home ranges (Gardiner et al. *in review,* b). Our results from modelling movement pathways support these findings, but also identify the amount of cover and vegetation structure in the local environment as being important factors that explain variation in behaviour of eastern bettongs.

Previous studies of habitat preferences of the eastern bettong suggested a lack of preference for particular floristics and vegetation structure (Johnson 1994b), however our study highlights behavioural responses to the density of vegetation at ground level and to tree-canopy cover. Denning was concentrated in areas with denser ground vegetation, provided by the presence of mat rushes *Lomandra*

longifolia and bracken fern *Pteridium esculentum*, but with relatively low tree cover. Bettongs den in nests that they construct from material such as grass, fibrous bark and bracken ferns. Their preferences for denning in dense vegetation may partly reflect availability of nesting material, but they are capable of transporting nesting material over quite long distances by carrying it in their prehensile tails, and they include material such as fibrous bark and fine tussock grasses that are not always available in the immediate vicinity of a nest. Bettongs may choose dense vegetation for nesting both to aid in concealment of the nest, particularly from aerial predators and also to hide the animal's escape if it is disturbed while in the nest.

Eastern bettongs foraged only in areas with woodland cover. This can be explained by the fact that the species feeds mainly on the sporocarps of ectomycorrhizal fungi (Johnson 1994), which associate with the fine roots of woodland trees and shrubs. Pasture soils are frequently fertilised and nutrient rich, unsuitable for ectomycorrhizal growth (Wardle *et al.* 2004) and therefore not useful as a resource for bettongs (Taylor 1992a). More open woodland are also associated with lower fertility soils, which are suitable conditions for ectomycorrhizal fungi networks, and can explain why foraging tends to occur further away from denser vegetation. Movement through denser vegetation is likely to be difficult where vegetation is often taller than the species.

Lastly, bettongs were likely to be travelling fast in more open areas with less cover. Similar movement patterns are expected to be observed when bettongs are moving through lower quality or less preferred habitat, particularly open pasture. Overall, our results show that the eastern bettong has a strong dependency on woodland vegetation communities, as they use all the woodland patches within their range, further suggesting that the total amount of habitat within their range is important. Preserving the total amount of woodland habitat can therefore be an essential management method for their persistence.

Within fragmented landscapes, the configuration of woodland patches varies, differing in sizes, shapes, distances from core habitat and state of degradation. Our study depicts how behavioural states change in fragmented landscapes, as a result of the attributes of the landscape. In less favourable environments, species tend to spend more time and energy searching for resources (Fahrig 2007b; Osbourn, Connette & Semlitsch 2014), and move at higher speeds (Graves *et al.* 2007; Braaker *et al.* 2014). Across our three sites, bettongs moved faster with longer step lengths when crossing lower quality (quantified as the density of regenerating stems, as an indication of regenerating and healthy woodland) areas such as open spaces, roads, and gaps between woodland through pasture. Interestingly, bettongs from the least fragmented site (Site 1) spent more time travelling fast than in the more fragmented sites. This could be a result of the woodland being of overall lower quality, combined with stressors such as the presence of grazing livestock, which are absent from the other two smaller and more fragmented sites, as these are strictly under covenant protection. Previous findings indicate that bettongs concentrate their home ranges in areas of higher quality (Gardiner et al. *in review, b*); this study further shows that concentrated movement - foraging and denning - occurs only in woodland, in areas of higher quality and usually within the larger remnant patches within a site.

Interestingly, bettongs used isolated elements within the landscape, such as small patches and stands of trees as stepping stones when travelling fast between larger woodland patches. This suggests that these isolated elements, that may not constitute suitable woodland patches for foraging or denning, can be important for movement within fragmented landscapes. Moreover, this also suggests that smaller patches can contribute to the amount of habitat available within a bettong's range, which was similarly reported by Gardiner et al. (*in* review, a, b). Thus, movement for a mobile species is not hindered by fragmentation if there is enough total habitat and if the gaps between patches are not too large. If gaps are too large, species are likely to be restricted to smaller amounts of habitat, and further influenced by edge effects, therefore restoring and retaining habitat, regardless of configuration, within a species range can be beneficial. Rather, habitat quality influences the frequency and type of movement. Low

quality habitats are likely to incur greater fitness costs, possibly threatening the persistence of populations within remnants over time (Robertson & Hutto 2006). Therefore, mitigating the impacts of degradation by including high-quality resources, managing grazing pressures and retaining woodland becomes more important as the rate of fragmentation increases.

It is common across taxa that males and females display different movement patterns, home ranges and area-use characteristics according to the resources that are important to their reproductive success (Harestad & Bunnel 1979). In mammals, males often have larger ranges to incorporate multiple females and avoid other males. Females are likely to concentrate their movement in areas of high food and shelter to meet their reproductive requirements (Lewis *et al.* 2006). In the eastern bettong, males were more likely to venture outside woodland in fragmented sites, while females tended to concentrate their movement within woodland, spending most of their time foraging. These sex differences highlight how each sex perceives habitat and, as an extension, how they use it. This is useful information for management to ensure that all resources are provided for successful reproduction and survival in both sexes. I did not differentiate between females with different ages and stages of young, or dispersal life stages such as weaned juveniles, however this could be useful information (Kokko & López-Sepulcre 2006) to manage essential habitat across all life stages. One caveat with movement modelling is choosing the correct number of states (Pohle *et al.* 2017), in this study I did not take into account individual heterogeneity which could have led models to favour a 3 state model over a 2 state model, however examining temporal structure and gamma distribution of all individuals, their movement was biologically better explained by 3 states than two.

Movement patterns provide a finer scale understanding of how animals perceive their habitat (Browning *et al.* 2018). Using Hidden Markov Modelling I was able to achieve this for the eastern bettong in a fragmented landscape. Our analysis reflect similar findings in Vernes and Haydon (2001) highlighted similar movement characteristics of a similar species, the northern bettong, in response to fire, being

able to identify area searching and how the bettong may exploit patches of food after a fire. Moreover previous home-range analyses (Gardiner et al. *in review, b*) also showed an importance for habitat quality and amount of habitat, but this study provides even finer scale information as to the attributes that drive movement patterns and where in the landscape different types of behaviours occur. None of these would be evident in less well-resolved analyses of movement. Even finer scale movements than was analysed, could potentially reveal individual foraging bouts or searching behaviour, obtained by programming even shorter time intervals of fixes. This study contributes to the larger body of work using HMMs as an easy and user-friendly method to analyse movement, and extending it for restoration and conservation purposes. This study shows HMMs could also be applied to species that are quite restricted in their habitat, however whether HMMs could work for even smaller species will rely on the resolution of tracking devices and complexity of habitat. HMMs work best with data that does not have large amounts of missing, or data is autocorrelated, as model selections often favour the most complex model, and therefore care needs to be taken when choosing the number of states. In this case I suggest following Pohle *et al.* (2017)'s pragmatic solution to identifying suitable states, but also use a priori knowledge to determine what is biologically relevant to the species and the study. There are analyses with stronger predictive power in determining behaviours such as machine learning (Börger 2016; Valletta *et al.* 2017), however these require substantial computational power and are often highly complex, therefore HMMs were more efficient for this study.

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4.7 Supplementary

Site	Frag. level	Quality	Woodland	Denning	Foraging	Travelling
1	Low	40	1290	0.07	0.53	0.4
2	Medium	106	85	0.06	0.72	0.22
3	High	117	157	0.19	0.66	0.15

Supplementary 1: Characteristics of each site and the proportion of locations recorded at each site. Quality as measured as the density of regenerating eucalypt stems, woodland is the area of eucalyptus woodland in hectares.

Density	1	1 to 2	1 to 3	2 to 1	2	2 to 3	3 to 1	3 to 2	3
1	0.6948635	0.079374	0.225763	0.9623675	0.000010	0.037623	0.283802	0.000043	0.716155
2	0.6183489	0.2731791	0.108472	0.00014348	0.999808	4.83E-05	0.007609	0.9918672	0.000524
3	0.3176661	0.6201988	0.0621351	0.00036023	0.999312	0.000328	0.956746	0.0097162	0.033538
4	0.2935931	0.6766378	0.0297691	3.64E-05	0.999934	2.97E-05	0.001845	0.998038	0.000117
5	0.3665472	0.605207	0.0282458	0.00015641	0.999724	0.000119	0.004592	0.9950543	0.000353
6	0.6494062	0.2558017	0.0947922	3.53E-05	0.999856	0.000109	0.001773	0.9980011	0.000225
7	0.5889754	0.2804557	0.1305689	0.00016287	0.99967	0.000167	0.986234	0.0014334	0.012333
8	0.6666664	2.75E-08	0.3333335	0.00787591	0.989074	0.00305	0.004803	0.995062	0.000135
9	0.3752657	0.5079104	0.1168239	0.00023539	0.999374	0.000391	0.00312	0.9967986	8.17E-05
female	0.8420377	0.090853	0.067109	0.886034	0.06175	0.052216	0.8694474	0.0436639	0.0868887
male	0.4269653	0.505908	0.067127	0.44603	0.382043	0.171928	0.2411653	0.1567168	0.6021179
cover	-	0.951873	-2.69535	-1.34802	-	-2.416253	-1.451458	1.389433	-

Supplementary 2: Transition probability matrix given the density of vegetation (low to high: 1-10), sex and percent cover.

5. General Discussion

Releasing Egbert, after being tracked for a month.
Photographer: *Cesar Penaherrera Palma*

5.1 Overview

Ecological restoration can be an effective tool to promote the persistence of biodiversity in fragmented landscapes. The main challenge for restoration ecologists is to understand how to successfully restore the elements of habitat that are needed to support biodiversity comparable to those in undisturbed ecosystems, and support ecological processes characteristic of those systems. Most restoration projects focus on the re-establishment of the most obvious structural elements of habitat (such as trees), but this does not always recreate the habitat conditions needed by animals (Suding, Gross & Houseman 2004). Restoring habitats that will sustain animal populations requires understanding what elements of habitat are essential for them – in other words, to adopt an animal-centred view of habitat (Jones & Davidson 2016b). The aim of this project was to do this for the eastern bettong in the Midlands bioregion, Tasmania. The region is a national biodiversity hotspot but is extensively fragmented, and has become a focus for restoration. Local non-government and government conservation organisations aim to restore native vegetation to improve habitat connectivity for native wildlife, particularly keystone species such as the eastern bettong. I used a multi scale approach, to determine the response of the eastern bettong, a woodland-dependant critical weight range (CWR) mammal, and an ecosystem engineer, across the Midlands bioregion to the fragmentation of woodland for agriculture. I determined their distribution at the landscape scale, investigated their ranging behaviours at the patch scale and obtained fine scale measures of the behavioural decisions of the bettong in relation to local environmental elements and landscape features. This provided a mechanistic understanding of how this species persists in relation to fragmentation of its woodland habitat for agriculture.

5.2 Summary of findings

Frameworks that seek to understand how species respond to fragmentation place varying importance on which landscape attributes are essential for persistence. I determined the distribution of the eastern bettong in the Midlands bioregion by assessing occupancy across woodland sites. Using single-species, multi-season occupancy modelling I found no influence of vegetation structure, presence of predators and landscape features on presence. The most important variable associated with occupancy of any woodland patch was the amount of accessible habitat in the immediately surrounding area. Habitat amount was more

strongly associated with occupancy than was the patchiness of that habitat, as defined by patch size and isolation. That is, the island biogeography model was not useful in accounting for variation in occupancy of the Midlands landscapes by the eastern bettong. The quality of habitat, indicated by the density of regenerating stems of overstorey stems, was also an important determinant of species presence. Given that the eastern bettong is a wide-ranging species for its body size and can cross gaps between woodland patches, all patches regardless of size can contribute to the total amount of habitat within a bettong's local landscape.

Fragmentation studies often focus on species richness and biodiversity, overlooking individual species' requirements. I wanted to provide an understanding of how eastern bettongs respond to landscape heterogeneity as revealed by individual movements. I tested the effects of habitat amount, fragmentation, population density and habitat quality on home-range size. These results show that bettongs focus their home ranges in higher-quality areas—that is, where stem density is higher, indicating higher biomass of fine roots and woodland health—and increase their home range size with increasing density and amount of woodland. All patches within a bettong's local landscape are important, but their use is likely driven by the quality of the habitat. Density estimates from the sampled sites showed strong variation, in which densities were higher in more continuous habitat, and decreased sharply as woodland area decreased, suggesting density and therefore population stability is limited by habitat area.

I used state-space modelling to examine the movement pathways of individual bettongs, so that I could identify how specific movement-behaviour states were affected by fine-scaled habitat variables including tree canopy cover, density of understorey vegetation and distance to edges of woodland patches. The analysis identified three distinct behaviour states, that were characterised as denning, foraging and travelling. The state-space approach revealed how transitions between behaviour states were affected by habitat variables, and to quantify individual variation in these responses (especially in relation to sex). This analysis was valuable in revealing how bettongs respond to their habitat in a way that would otherwise be possible only by continuous direct observation of animals through their entire activity cycle – which would be an impossible task, especially for a nocturnal, cryptic and fast-moving animal like the eastern bettong. This analysis resulted in several novel findings. Bettongs denned near the edges of larger high-quality patches in places where ground-level density of vegetation is high but tree canopy cover is low. Foraging was concentrated in areas with high tree canopy cover and lower density of ground-level vegetation. When

transiting between patches, bettongs used smaller and degraded patches as stepping stones. Finally, the proportion of time spent by bettongs in each behaviour differed across sites, such that bettongs in areas where habitat quality was lower spent more time in fast travel relative to foraging. This analysis supported findings of the other studies within this thesis, but the much higher resolutions provided additional insight into how individual bettongs respond to specific habitat features. The study was the first application of state-space modelling, based on high intensity GPS tracking, in a small terrestrial mammal, and points to a more extensive application of this analytical approach in terrestrial animal ecology.

5.3 Where to restore: Increase total habitat amount

Each framework, the island biogeography theory, habitat amount hypothesis, and habitat continuum theory attempt to explain the impacts of fragmentation on species, but differ in which attributes are important for persistence. Habitat fragmentation will affect species differently according to their habitat requirements and movement patterns. The eastern bettong is a relatively mobile species and is able to utilise multiple patches within its range, therefore the habitat amount hypothesis better explains its distribution (Fattebert *et al.* 2017). As a woodland specialist, bettongs do not make extensive use of the matrix as habitat and therefore the habitat continuum theory is not applicable. These results do not refute the island biogeography theory and related hypotheses. Rather, they suggest that the theory is applicable to more sedentary or low mobility species, as supported in species of plants and arthropods (Evju & Sverdrup-Thygeson 2016; Haddad *et al.* 2017), that are more likely to be affected by isolation and patch size. Each of the three frameworks is likely to be appropriate at different spatial scales and for different species. The habitat amount hypothesis may be more applicable to species that are both mobile and habitat specialists, that have the ability to move between and use multiple patches but do not make use of the matrix for foraging or denning.

My research supports the recent theories put forward by Fahrig *et al.* (2019), suggesting habitat fragmentation may not be negative per se. The eastern bettong was able to cross gaps and even compensate for fragmentation by increasing its home range size. By removing the strict delineation of patches and testing the effects at the landscape scale, the habitat amount hypothesis values smaller patches, which are often disregarded or considered unusable (Fahrig 2013). Small patches can contribute to the total amount of habitat

available which can be valuable for movement (Barbosa *et al.* 2017), resting, and refuge in the matrix (Machado *et al.* 2016). This suggests that mobile species can cope with a certain degree of fragmentation if they can access enough habitat within their range. Of course, this applies to the places in the Midlands where there is sufficient habitat for bettong populations to persist. There are large areas of the Midlands where bettongs were not found in the woodland remnants. In these parts, there may not be sufficient habitat within an area that a bettong could energetically include in its home range for bettong populations to be able to persist.

It is imperative that by increasing habitat amount, it is also improving connectivity to promote population mixing via migration or dispersal, decreasing edge effects, and therefore reduce the risk of local extinctions. The use of corridors, has been beneficial for increasing habitat amount however the overall success of corridors relies on its quality, composition and whether species can use them without becoming an ecological trap (Hinsley & Bellamy 2000; Bailey 2007). Stepping stone habitats, especially for mobile species, can promote connectivity by sustaining subsets of populations and decrease the distances to travel between patches as demonstrated in woodpeckers (Saura, Bodin & Fortin 2014). Restoring habitat to improve connectivity will rely on understanding species use of habitat, as I have done in this study, but extending the focus towards understanding what elements will promote movement between populations, for example improving matrix quality, increasing habitat amount near high quality habitat, and or providing more resources such as refuges (Fahrig 2001; Donald & Evans 2006). Within my findings, small stands of trees and low ground cover appeared to promote the movement of bettongs between patches, whether this is sufficient at the landscape level is yet to be explored. Further work including, landscape genetics (unpbl. Kirstin Proft) and the influence of local and landscape elements will elucidate to how much and what type of habitat structure or quality is needed.

Importantly, the density of bettongs in woodland remnants in the Midlands, even when the amount of habitat available was taken into account, showed that bettong abundance was much lower in remnants than in intact, contiguous woodland habitat on the edges of the Midlands. Fragmentation can result in the reduction of habitat quality overall and in the sparsity of high quality habitat. The remnant patches of habitat are therefore less able to support the same densities as more intact remnants, resulting in low population densities. Thus, bettongs may not be directly affected by fragmentation where there is sufficient total amount

of habitat in a local area, as supported by the work throughout this thesis, but populations are at risk of lower quality habitat as a result of fragmentation.

5.4 What to restore: Quality of habitat

Habitat degradation is often considered secondary to habitat loss and fragmentation. This is certainly the case for bettongs, which have disappeared from much of the Midlands where 87% of woodland cover has been removed for agriculture. Within the extent of fragmentation of the patches that I studied, where bettongs are still able to persist, these results highlight the importance of patch quality over fragmentation *per se* for the presence and habitat use of bettongs, noting that density in remnants was quite low compared to populations in intact woodland. In my study, the variable that indicated quality was the stem density of regenerating trees. Stem density is a good indicator for woodland health, displaying the recruitment of canopy and mid-storey trees, and therefore the presence of a seed bank suitable for regeneration. It also suggests a higher biomass of finer roots and associated ectomycorrhizal fungi- upon which bettongs feed. Lastly, with higher stem density, it is likely that there is little impact from disturbances such as grazing and fire which can impact regeneration, therefore sites with high stem density retain some quality and potential for tree regeneration.

Restoring vegetation that can encourage higher biomass of fine roots can be important in providing foraging opportunities and secondary benefits to plant communities within the ecosystem. Low quality habitats provide lower quality resources, influencing movement, population density and viability. If quality is not restored, habitats can become ecological traps or render patches unusable (Taylor 2017), ultimately losing ecological value in the landscape (Hale & Swearer 2017). Habitat quality is species specific, therefore using an animal centric approach can identify what attributes a species values, which has important management implications.

Habitat degradation is amplified by disturbances, threatening the viability of habitats over time. In agricultural landscapes like the Midlands, grazing pressures and changed soil conditions contribute to degradation. Soil compaction increases soil hardness and modifies soil composition, which make it unsuitable for the recruitment of native plant species (Bailey, Davidson & Close 2012; Collins & Fahrig 2017), or digging by animals like the eastern bettong. Moreover, in agricultural dominated landscapes, the high input of

pesticides and fertilisers changes the nutrient composition of the soil, often resulting in the loss of ectomycorrhizal fungi and a shift towards bacteria-dominated soils. Such soils are associated with fast nutrient cycling, appropriate for agricultural plant species but not woodland plant species (Bardgett *et al.* 2005; Strickland & Rousk 2010; Van Der Heijden 2010), impacting remaining native vegetation persistence. Occupancy modelling showed that bettongs were found only in or near patches of woodland which were under covenant or reserve protection. These woodland patches have been fenced off and cannot be modified by human activity, therefore retaining some soil and vegetation quality. I suggest that covenants and reserves can be important areas in the landscape to use as focus points for restoration, and promote the connectivity of high-quality habitats.

Lastly, this study was the first to my knowledge, to use state space modelling to obtain a species perception of fragmentation. Fine scale knowledge of small animals is difficult to obtain due to their cryptic nature and the size constrictions of tracking devices. Knowledge of habitat use of smaller species at finer scales is often lacking and can result in inefficient management of their habitat. Using Hidden Markov Modelling, I show that it is possible to identify behavioural states and the processes underlying transitions for small species, including other critical weight range mammals. I were able to highlight habitat attributes and differences in movement across individuals and within fragmented sites. Previous studies suggested that the distribution and abundance of eastern bettongs was not influenced by floristics and habitat structure (Taylor 1993a; Johnson 1994a). However, the movement and tracking data shows ground-level vegetation such as bracken fern *Pteridium esculentum* and mat rushes *Lomandra longifolia* are important for providing denning areas, while woodland cover was important for foraging. It was also clear that when crossing gaps, bettongs readily used areas with denser ground layer vegetation or small stands of trees as stepping stones. In agreement with occupancy and home range findings, there is support for the concept of total habitat amount and quality being important components of habitat for species movement. The results from this study provided finer scale information to highlight where these states occurred and why, which is often overlooked in traditional estimations of movement. For a mobile species, restoration efforts should focus on increasing habitat amount, restoring ground level vegetation to provide denning resources, and retaining smaller patches to aid crossing gaps. Future work could implement state space modelling on a variety of terrestrial

species with the capacity to be fitted with tracking devices, to gain common attributes important for multiple species rather than focusing on vegetation as a means for restoring biodiversity.

5.5 The persistence of eastern bettongs

Unlike other critical weight range mammals, such as the eastern barred bandicoot (*Perameles gunnii*), the eastern bettong still persists in local populations across the Midlands bioregion. This is probably due to the retention of high quality, dry sclerophyll, woodland by means of covenant protection. The mobility of eastern bettongs facilitates their use of neighbouring patches and allows them to gain access to more resources. Therefore, they are less negatively impacted by habitat fragmentation than are smaller ranging species like bandicoots. The bandicoot is a slower moving critical weight range mammal which prefers to forage in open grasslands, making them more susceptible to predation by feral cats. As such they are more impacted by habitat loss and predation.

Interestingly, the Midlands has a high density of feral cats (R. Hamer, unpublished) but I frequently recorded bettongs using the same woodland remnants as cats. Feral cats are capable of taking down prey much larger than bettongs, like pademelon (Fancourt 2015), and therefore could easily predate on bettongs. It is possible that the presence of preferred prey items such as the introduced European rabbit and black rat, that are both much more abundant and potentially easier to subdue provide better feeding opportunities. On the mainland, decline of bettong populations is mainly attributed to the presence of the red fox (Johnson 2006), which are not present on the island of Tasmania. Although the bettong is persisting in the Midlands, caution is required as density estimates of bettongs show significant declines in decreasing habitat areas. Further loss and degradation of remaining woodland will increase the risk of local extinctions. The persistence of bettongs relies on restoring and retaining woodland patches and increasing quality by promoting the recruitment of mycorrhizal fungi.

5.6 Future directions and Conclusion

With increasing human resource demands, the socio-economic value of agriculture and climate change the challenge to maintain biodiversity will increase (Tilman *et al.* 2017). Using an animal-centric

approach at various spatial scales, I provided a mechanistic approach towards managing and restoring habitat. Using a multi-scale approach helped understand species response by unveiling what landscape and local elements, are important for a species persistence. This can direct management efforts towards investing their restoration efforts at the appropriate scale. Within my study, at the landscape scale habitat management should focus on increasing total habitat amount, while at the patch scale improving the quality of habitat and providing ground vegetation cover. These methods can be readily applicable to all biodiversity persisting in fragmented landscapes, and therefore further our understanding of species requirements. Like Hodgson *et al.* (2011), our study highlights focusing and managing habitat amount and quality as a priority for conservation. As the practice of restoration grows, there is a need for an experimental focus to evaluate the effectiveness of management, requiring a combination of effort from conservation and management. I encourage future experimental approaches to conceptualise patch quality and drivers of survival, such as mapping food distribution, predator interactions, and disturbances. Integrating knowledge and approaches across the fields of restoration, movement and landscape ecology will improve ecological knowledge of species-habitat interactions and quantify restoration actions. Restoration is an extensive process and its success relies on long term monitoring (Ruiz-Jaen & Mitchell Aide 2005), therefore I strongly recommend regular monitoring programs to evaluate and adjust management as needed.

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